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THE UNIVERSITY OF ALBERTA

METAZOAN PARASITES OF FISHES OF COLD LAKE, ALBERTA:
A COMMUNITY ANALYSIS

by

RAYMOND LEONG TAK SENG

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
FALL, 1975

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, ~~and~~ recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Metazoan parasites of fishes of Cold Lake, Alberta: A community analysis" submitted by Raymond Leong Tak Seng, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Thirty-seven species of parasites from lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*), lake trout (*Salvelinus namaycush*), coho (*Oncorhynchus kisutch*), northern pike (*Esox lucius*), white sucker (*Catostomus commersoni*), longnose sucker (*Catostomus catostomus*), burbot (*Lota lota*), ninespine stickleback (*Pungitius pungitius*), and walleye (*Stizostedion vitreum*) were recovered from Cold Lake, Alberta. Thirty-two species of parasites matured in one or more of these species of fishes.

Metechinorhynchus salmonis was the most dominant parasite, infecting all ten species of fishes. The superabundance of this acanthocephalan affected the whole parasite community, resulting in high similarity between communities of parasites in whitefish, trout, coho, and burbot. The majority of the other fish hosts were characterized by parasites specific to them. The communities of parasites in whitefish and cisco appear to be relatively diverse, but the communities of parasites in the other fishes appear to be of low diversity when compared with the parasites of the same species of host studied elsewhere.

In whitefish and cisco, the number of species of parasites and the number of individual parasites per fish increased with age (except in the oldest age class), but the diversity of the parasite community decreased. Individual species of parasites in whitefish or cisco showed definite seasonal patterns of abundance and/or reproductive activity. Most species reproduced during the late spring or summer, but most species reached maximum abundances in early winter. The parasite fauna of the fishes were not obviously correlated with their food habits, due at least

in part to differential importance of various food items for the transmission of parasites.

The dominance of *M. salmonis* within the entire community of parasites was due to its wide host range, it being primarily a parasite of the dominant salmonid fishes, its use of transport hosts as an alternate route in its life cycle (allowing it to reach its piscivorous hosts), and its method of population control. There appeared to be a feed-back mechanism in whitefish which controlled the number of gravid females, thus the egg production. Combined with the high proportion of acanthocephalans in whitefish, this appeared to control the acanthocephalan population within the entire ecosystem.

The parasite community acquired by the introduced coho was similar to that of the native salmonid fishes, and was dominated by *M. salmonis* *Ergasilus auritus* and *E. nerkae*. *Philonema agubernaculum* and *Cystidicola stigmatura* were found only in overwintered coho.

There was considerable exchange of parasites among the salmonid fish species in Cold Lake. The species of parasites exchanged can be considered to be typical of salmonids, particularly of whitefish and cisco. The exchange of parasites among the non-salmonid fishes was more restricted, and appeared to involve primarily immature and larval stages for which the hosts acted as transport or intermediate hosts.

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I. INTRODUCTION

There are numerous lakes in Alberta, varying from shallow, very eutrophic prairie lakes with warm summer temperatures and no thermal stratification, to deep, cold, oligotrophic, high-altitude lakes. Included are several large, deep, oligotrophic lakes containing populations of relict invertebrates such as *Mysis relicta* and *Pontoporeia affinis*. Although the number of species of fishes in Alberta is relatively low (Paetz and Nelson, 1970), this last group of lakes contains the largest number of species (Appendix II in Paetz and Nelson). Cold Lake, in northeastern Alberta, is one of these lakes, and contains 25 species of fishes (Roberts, 1975). Included are three species of native salmonids, lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*) and lake trout (*Salvelinus namaycush*).

In the spring of 1970, the Alberta Fish and Wildlife Division began a three-year experimental program of stocking Cold Lake with coho salmon (*Oncorhynchus kisutch*) to provide increased sport fishing. As a part of this program, the Fish and Wildlife Division set gill nets at various parts of the lake to study the distribution of the coho. Coho taken during this study of distribution were heavily infected with parasitic copepods (*Ergasilus* spp.) and acanthocephalans (*Metechinorhynchus salmonis*). Mr. M. R. Robertson of the Fish and Wildlife Division, at St. Paul, Alberta, requested the University to undertake a study of the importance of these parasites.

Relatively little is known about the parasites of the fishes of Alberta. No comprehensive surveys have been made of the parasites of the fishes of any lake in the province. Miller studied the taxonomy, life history and control of *Triaenophorus* spp. (summarized in Miller, 1952). Price and Arai (1967) and Arai and Chien (1973) have surveyed the monogeneans of fishes from southern Alberta, Arai and Kussat (1967) investigated the effect of domestic and industrial effluents on the parasites of catostomid fishes in the Bow River near Calgary, and Mudry and Arai (1973a, b) have investigated the life history and population dynamics of *Hunterella nodulosa* in catostomid fishes. The only other published information on the parasites of fishes of Alberta are miscellaneous observations summarized in Paetz and Nelson (1970).

Previous studies in parasitology at this University, particularly that of Neraasen (1970), have illustrated the value of measures used in general ecology, such as indices of diversity and similarity, for the study of the circulation of parasites among related hosts. Wisniewski (1958), Chubb (1963a, 1970), Esch (1971) and Esch *et al.* (1975) have all indicated that the circulation of parasites is dependent upon interactions within the entire ecosystem, and should be studied using an ecosystem (or at least a community) approach. To do so requires information on the relative abundances of the hosts and of the parasites; for the latter, data are required on intensity of infection, as well as prevalence. Most of the large-scale surveys that have been done have not provided such information. Cold Lake, with its variety of fishes, and especially its abundant populations of salmonids, made an ideal site for such a study.

The community of parasites in any ecosystem is affected not only by the complex of host species available, but also by various modifying factors such as the age of the hosts, seasonal patterns, and dietary habits of the hosts. Most species of parasites that have been studied have shown an increase in abundance with age of host (Thomas, 1964; Chappell, 1969b; Pennycuick, 1971b; Anderson, 1974; Hine and Kennedy, 1974b), probably due to the consumption of greater amounts or kinds of food. Seasonal changes in the abundance or maturation of parasites have been attributed, at least in part, to temperature (Chubb, 1963b; Awachie, 1965; Kennedy, 1968, 1969; Kennedy and Hine, 1969; Pennycuick, 1971a; Bibby, 1972; Lien and Borgstrom, 1973; Anderson, 1974). There have been very few studies on the seasonal distribution of parasites in lakes which freeze over in winter (Tedla and Fernando, 1969; Cannon, 1973), and none of these deal with communities of parasites.

Although coho salmon have been stocked in many freshwater lakes in North America in recent years (Tody and Tanner, 1966; Becker and Brunson, 1968; Klein and Fennell, 1969; Avery, 1973; McKnight and Serns, 1974), there have been no adequate investigations of the parasites of those coho, and only two reports of incidental observations on their parasites (Becker and Brunson, 1968, reported sporadic infections with plerocercoids of the bass tapeworms, *Proteocephalus ambloplitis*, and Klein and Fennell, 1969, reported two species of endoparasites). The request by Mr. Robertson provided an opportunity to study the acquisition of parasites by coho in a lake with a community of fishes including substantial populations of native salmonids.

Preliminary investigation showed that the acanthocephalan, *Metechinorhynchus salmonis*, was found in large numbers not only in the introduced coho, but also in a wide variety of native fishes. This acanthocephalan has been found in other surveys of fishes, but never in such high numbers (Dogiel, 1961; Tedla and Fernando, 1969, 1970;

Dechtiar, 1972; Collins and Dechtiar, 1974).

The aims of my study, therefore, were:

1. To determine the community of parasites in a community of fishes and the patterns of their circulation.

2. To determine the effects on the community of parasites of modifying factors: a) age, b) season, c) diet.

3. To determine the parasites acquired by the introduced coho salmon and the role coho played in the circulation of parasites.

4. To investigate aspects of the biology of the dominant parasite, *Metechinorhynchus salmonis*, to determine the reasons for its dominance, its pattern of circulation within the fishes in Cold Lake, and, if possible, its basic population dynamics.

II. STUDY AREA

Cold Lake is a large (surface area, 373 km^2), deep (mean depth, 60 m; maximum depth, 100 m), oligotrophic lake located about 290 km (180 miles) northeast of Edmonton, on the Alberta-Saskatchewan border. It drains eastward into Hudson Bay via the Cold River and the Churchill River system. It is fed by two rivers, the Martineau River from the north and the Medley River from the northwest. A map of Cold Lake, giving depth contours, is shown in Figure 1. Paetz and Zelt (1974) gave additional details of the morphometry, physical, chemical and some biological characteristics of Cold Lake.

The annual cycle of water temperature (exemplified by my records of temperatures in North Bay) consists of a four-month warming period (May through August), a four-month cooling period (September through December), and a period of low, stable temperature (January to April) (Figure 2). During the summer, surface water temperatures rise rapidly to a maximum of about 18 C in August. Paetz and Zelt (1974) reported that thermal stratification was pronounced during the summer, with the thermocline 9-15 m deep in July and 15-21 m deep in August, with hypolimnetic temperatures of 4.5-8.5 C. Most of my summer recordings from North Bay appear to be epilimnetic.

The lake usually froze over by the third week of December and broke up about the last week of May. Paetz and Zelt (1974) pointed out that the annual period of ice cover (mean, 147 days) was substantially shorter than that of other lakes in Alberta, and resulted from a delayed

Figure 1. Bathymetric map of Cold Lake (Department of Agriculture, Government of Alberta) showing sampling locations. (Depth contours are in feet.)

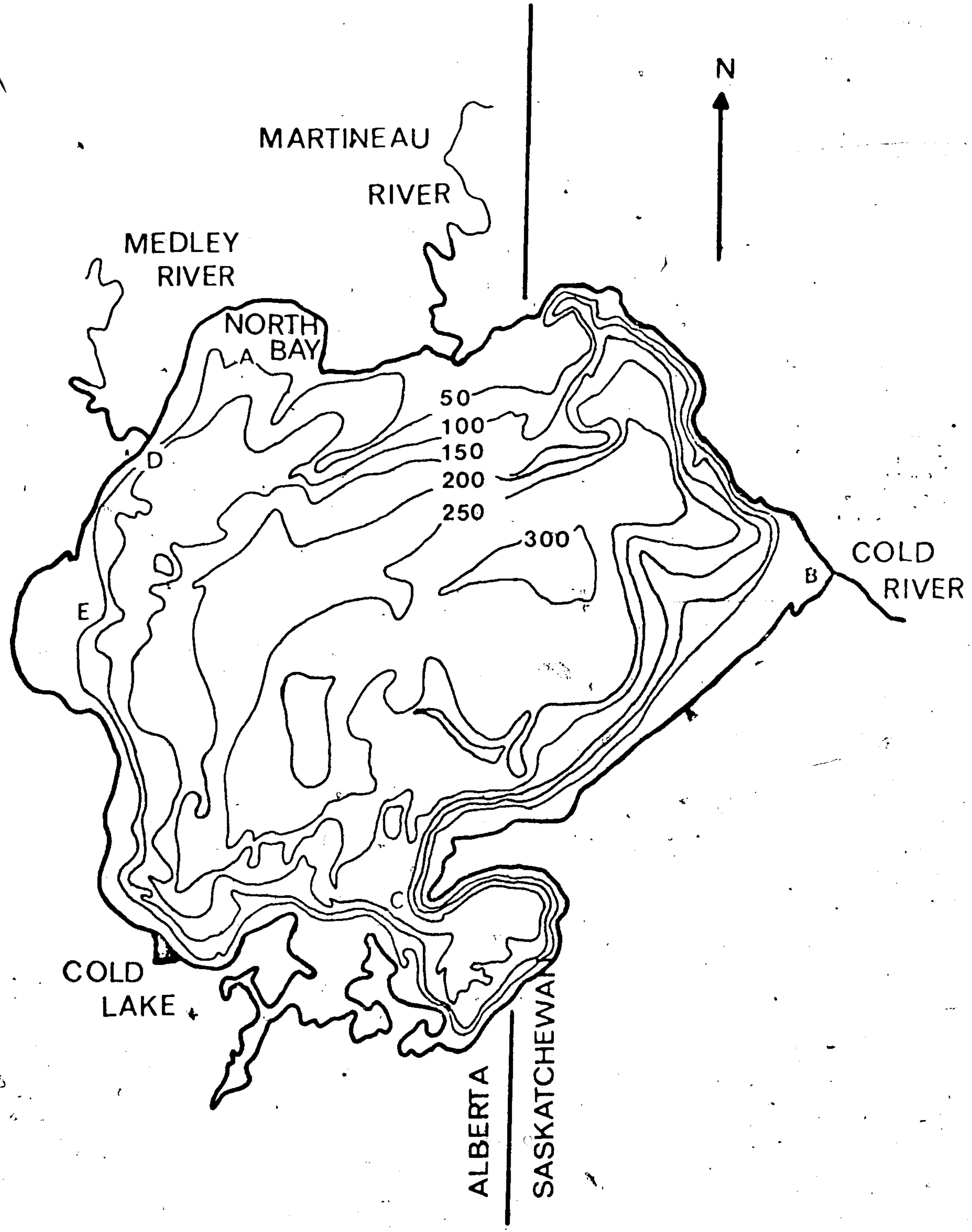
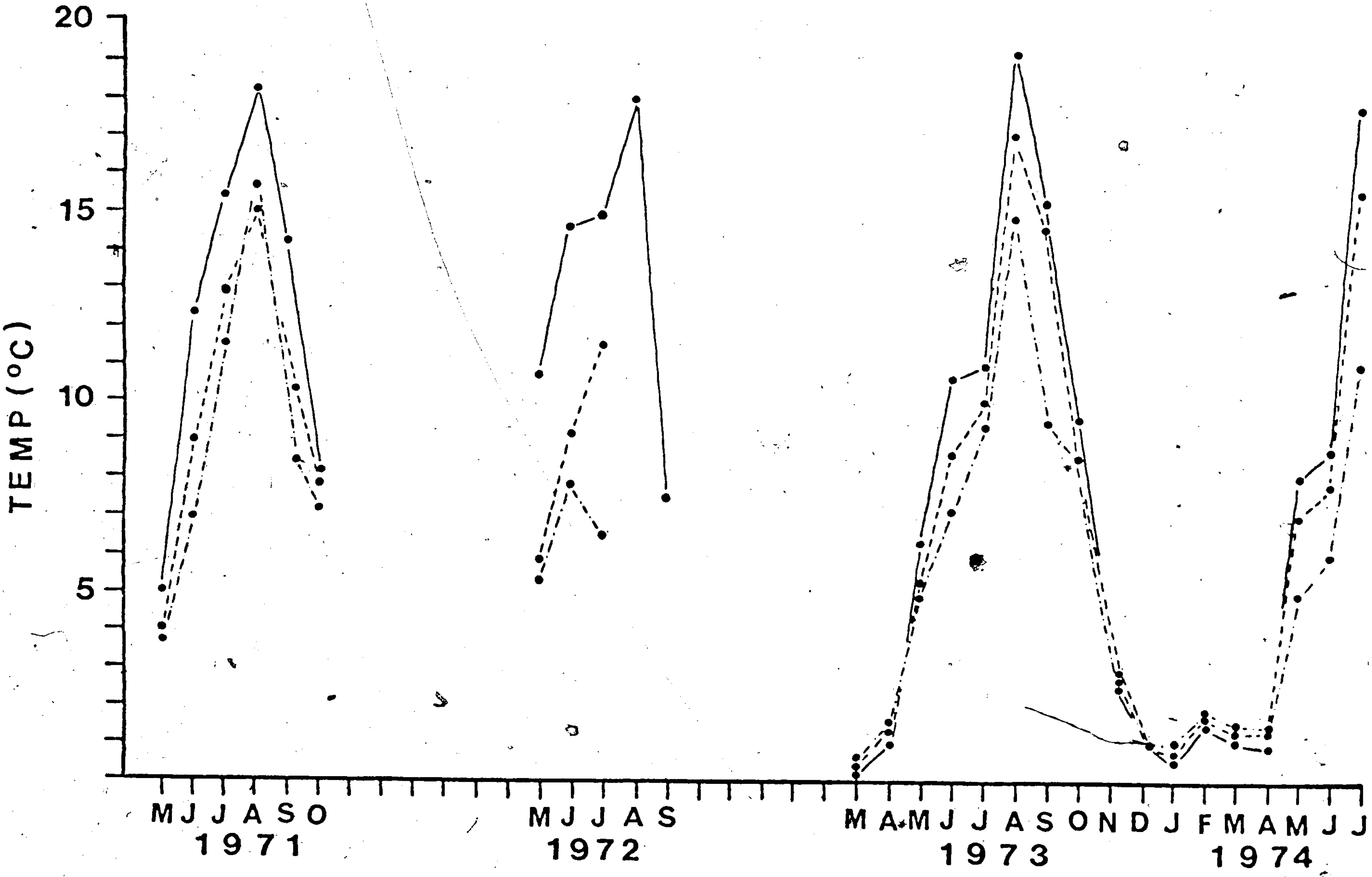

N
MARTINEAU
RIVER
MEDLEY
RIVER
NORTH
BAY
A
50
100
150
200
250
300
D
E
B
COLD
RIVER
C
COLD
LAKE
ALBERTA
SASKATCHEWAN

Figure 2. Water temperatures at the surface (————), 5 m (--------), and 10 m (-·-·-·-·) at North Bay, Cold Lake, Alberta


TEMP (°C)
20
15
10
5
M J J A S O
1971
M J J A S
1972
M A M J J A S O N D J F M A M J J
1973
1974

freeze-up due to the greater depth and consequent slower cooling of Cold Lake.

Except for records of the presence of the relict species *Mysis relicta* and *Pontoporeia affinis* (Paetz and Zelt, 1974) the invertebrate fauna of Cold Lake has not been studied. From an examination of fish stomachs, the lake appears to have relatively large populations of amphipods, particularly *Pontoporeia affinis*, copepods, mayfly larvae and chironomid larvae.

Paetz and Zelt (1974) reported 18 species of fishes in Cold Lake; Roberts (1975) reported 25 species. The composite list is shown in Table 1. All of the cyprinids, plus *Percopsis omiscomaycus*, *Culaea inconstans*, *Etheostoma exile*, *Percina caprodes*, and *Salmo gairdneri*, were found primarily along rivers or in shallow, heavily vegetated inlets, and were not included in this study. The other fishes were found mainly in the lake. All of the latter (except for *Perca flavescens*, found primarily in the shallow southern part of the lake, and *Cottus cognatus*, widely distributed, but sparse, in the lake, and not catchable by the methods I employed) were included in the study. The following notes on each of these species are taken from Scott and Crossman (1974), from Roberts (pers. comm.), or from my general observations at Cold Lake. Detailed information on the food habits of these fishes will be presented in a later section.

Lake whitefish (*Coregonus clupeaformis*) are bottom feeders which are widely distributed throughout Cold Lake, at various depths, most of the year. In July and August, they move into deeper, cooler water, and in late October and November, at a time when the water temperatures are

Table 1. Species of fishes and their relative abundances in Cold Lake, Alberta. Data are from Roberts (1975) and Paetz and Zelt (1974). Where they differ, data from Paetz and Zelt are in parentheses.*

Fish species	Common name	Relative abundance
Salmonidae		
Thymallus arcticus (Pallas)	Arctic grayling	I^{-}
Coregonus clupeaformis (Mitchill)	Lake whitefish	+++
C. artedii LeSueur	Cisco	++++
Salvelinus namaycush (Walbaum)	Lake trout	++
Salmo gairdneri Richardson	Rainbow trout	I^{+} (-)
Oncorhynchus kisutch (Walbaum)	Coho salmon	I^{++}
Cyprinidae		
Couesius plumbeus (Agassiz)	Lake chub	++ (+)
Notropis hudsonius (Clinton)	Spottail shiner	+++
N. atherinoides Rafinesque	Emerald shiner	++
Pimephales promelas Rafinesque	Fathead minnow	++
Chrosomus neogaeus (Cope)	Finescale dace	+ (-)
Semotilus margarita (Cope)	Pearl dace	+ (-)
Rhinichthys cataractae (Valenciennes)	Longnose dace	+ (-)
Percidae		
Etheostoma exile (Girard)	Iowa darter	+
Perca flavescens (Mitchill)	Yellow perch	++
Percina caprodes (Rafinesque)	Logperch	+ (-)
Stizostedion vitreum (Mitchill)	Walleye	++
Gasteroteidae		
Culaea inconstans (Kirtland)	Brook stickleback	+
Pungitius pungitius (Linnaeus)	Ninespined stickleback	++++(++)
Catostomidae		
Catostomus catostomus (Forester)	Longnose sucker	++
C. commersoni (Lacepede)	Whitesucker	+++ (++)
Esocidae		
Esox lucius Linnaeus	Northern pike	+++
Percopsidae		
Percopsis omiscomaycus (Walbaum)	Trout-perch	+ (++)
Gadidae		
Lota lota (Linnaeus)	Burbot	+++
Cottidae		
Cottus cognatus Richardson	Slimy sculpin	++ (+)

*+ rare, ++ common, +++ abundant, ++++ very abundant, I introduced, I^{-} unsuccessful introduction.

falling, they move into shallow water or the rivers to spawn.

Cisco (*Coregonus artedii*) are schooling pelagic plankton feeders, often observed at the surface in the early evening during the summer. The population in Cold Lake is a dwarf one, which is preyed upon by several predators. They spawn in shallow water in the fall.

Lake trout (*Salvelinus namaycush*) are active predators on other fishes, particularly sticklebacks and cisco. They feed in shallow water, except during July and August when they remain in the cooler, deeper waters. They spawn in relatively shallow water in the fall.

Two-year old fingerling coho (*Oncorhynchus kisutch*) were introduced into Cold Lake via the Medley River each spring from 1970 through 1972. Each fall, from 1971 through 1973, three-year old potential spawners were trapped as they returned to the Medley River. They were distributed mainly along shallow sandy bays and near river outlets (Roberts, pers. comm.). They fed on a variety of food, particularly aquatic insects and sticklebacks.

Walleye (*Stizostedion vitreum*) feed on a variety of fishes depending on their availability. They spawn in late spring or early summer.

Ninespine sticklebacks (*Pungitius pungitius*) spawn in early summer. During the breeding season, they swim in large schools in shallow water and are extensively preyed upon by lake trout and pike. After spawning, they disperse into deeper water. The food consists mainly of small crustaceans and aquatic insects.

Both longnose suckers (*Catostomus catostomus*) and whitesuckers (*C. commersoni*) are spring-spawning bottom feeders. The food of both suckers consists mainly of chironomid larvae. During the summer, white-suckers favour warm shallow waters, while longnose suckers favour colder parts of the lake.

Northern pike (*Esox lucius*) are opportunistic predators which feed on a large variety of fishes. They are widely dispersed in the lake, with their highest populations in shallow weedy bays or in heavily vegetated rivers. They spawn in very shallow areas, especially along rivers, soon after those areas open up in the spring.

Burbot (*Lota lota*) are deep-water, night-feeding, voracious predators. Small individuals, such as those in Cold Lake, feed on a wide variety of organisms, including amphipods and various small fishes. Larger individuals feed almost exclusively on fishes. They spawn in mid-winter.

III. MATERIALS AND METHODS

Samples of fishes (except sticklebacks) were obtained by gill-netting. (Throughout this thesis, "fishes" will be used for species, "fish" for individuals.) Nets of 37 mm mesh were used for cisco, nets of 62 or 100 mm mesh for the other species. Samples of whitefish were collected monthly from June to October, 1971, and from March, 1972 to July, 1974. Samples of cisco were collected monthly from June to October, 1971; May to September, 1972; and March, 1973 to July 1974. All were collected from sets in North Bay (area A in Figure 1). Coho salmon were obtained from June to October, 1971; April to November, 1972; and September to November, 1973, from sets at various locations in the lake (areas A-E in Figure 1). Pike, burbot, lake trout, walleye, longnose sucker and whitesucker were necropsied whenever they were gillnetted. Walleye were obtained primarily from sets near the Cold or Medley Rivers (areas B and D), the others were more widely distributed.

Samples of sticklebacks were obtained by seining near the Medley River (area D), by minnow-trap (areas C and D), or from the stomachs of trout and pike (various locations).

The weight, fork length and sex of each fish were determined. Ages were determined from scales taken from above the lateral line below the dorsal fin. The external surfaces were examined macroscopically for ectoparasites. Gills and viscera were removed and immediately examined for metazoan parasites using standard procedures, or were frozen and examined later.

Nematodes were relaxed and killed in glacial acetic acid, copepods were relaxed and killed in water, and both were preserved in 5% glycerine-alcohol. Trematodes, cestodes and acanthocephalans were relaxed and killed in water and preserved in AFA (Meyer and Olsen, 1971). Unfixed cestodes were stained with Blachin's lactic acid carmine stain (Reichenow *et al.*, 1952), fixed cestodes and trematodes with Semichon's acetocarmine; all were mounted in Canada balsam. Nematodes and acanthocephalans were cleared in lactophenol and examined in temporary mounts.

Food items recovered from the stomachs were identified, and the number of each type of fish prey recovered from the stomachs of the predators was counted. The prevalence of each item was used as an indication of its importance in the diet.

The measure of the size of the population of a parasite used in this thesis is a product of prevalence (percent of the sample infected) and the mean intensity (mean number per infected fish, $\bar{N}$) of the parasite, termed the "abundance."

The relative importance of each parasite species in an individual species of fish was measured by a simple dominance index ($D_i = 100P_i$), where P_i is the proportion of parasite i, measured as the abundance of parasite i divided by the sum of the abundances of all parasites in that host species).

Two dominance indices for each parasite species in the whole fish community were calculated. An unweighted dominance index was obtained for each parasite by summing the abundances of that parasite across all host fishes, and dividing by the grand sum of the abundances of all parasites in all host fishes. A weighted dominance index was obtained in the same way, except that before summing, the abundance of each parasite in each species of fish was adjusted by multiplying it by a weighting factor which estimated the relative abundance of that host species.

The weighting factor was determined as follows: Records of locations sampled, sizes and lengths of nets set and fish caught during extensive sampling programs conducted from June 25, 1970 to February 4, 1971, May 19, 1971 to November 5, 1971, and May 18 to September 5, 1972 were obtained from Fish and Wildlife Division, St. Paul. The number of each species of fish caught per 10^6 m^2 of nets was calculated, then adjusted to a ratio, with the value for cisco set equal to 100.

Nets were set in widely scattered areas; there was no apparent area selectivity for particular host species. Nets were mostly small mesh (37 to 62 mm), set in shallow water areas and mainly in the upper or middle of the column of water. Thus, the mesh size, depth and the height in the column where nets were set were important in determining the numbers and types of fish being caught. The ratio for each fish species was then adjusted by a multiplication factor obtained by a subjective estimation of the degree to which the nets were selective for or against that particular fish species. For most species, the resulting estimate of relative abundance was consistent with the estimates in Table 1. For longnose suckers, however, the value was considered to be too high, and the multiplication factor was arbitrarily reduced. The relative abundance of ninespine sticklebacks was subjectively estimated from seining, trapping and personal observations. This whole procedure is summarized in Table 2.

Various measures are used to compare parasite communities in different fishes, in fish of different ages, or in fish taken at different seasons. These measures are:

Table 2. Summary of procedures used in obtaining a weighting factor for the relative abundance of the fishes examined

	Whitefish	Cisco	Trout	Coho	Pike	Whitesucker	Longnose sucker	Burbot	Stickleback	Walleye
No. fish/10^6 m^2	9.27	324.7	0.25	0.13	0.96	3.53	1.8	0.21		0.49
Ratio	2.85	100	0.08	0.04	0.30	1.09	0.55	0.06		0.15
Net selectivity										
Mesh size	-	+	+	+	+	-	-	-		+
Depth of water	-	+	±	+	±	±	±	-		-
Column of water	-	+	-	+	+	+	-	-		+
Multiplication factor	10	1	2	1	2	2	2	10		2
Weighting factor	28.5	100	0.16	0.04	0.06	2.18	1.1	0.6	60	0.3

1. the number of fish examined (n),
2. the number (S) and mean number ($\bar{S}$) of species of parasites recovered,
3. the total number of individuals of all species of parasites (N) in the sample and the mean number of individuals of all species per infected host ($\bar{N}$),
4. the Shannon-Weaver index of diversity (H') (Shannon and Weaver, 1949), calculated as:

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

where P_i = the proportional abundance of parasite i (as above), and ln = natural logarithm,

5. the reciprocal of Simpson's index (SI) (Simpson, 1949), calculated as:

$$SI = \frac{1}{\sum_{i=1}^{S} (P_i)^2}$$

6. an index of evenness (E) (Hurlburt, 1971), calculated as:

$$E = \frac{H' - H'_{min}}{H'_{max} - H'_{min}}$$

where $H'_{min} = \ln N - \frac{N - S + 1}{N} \ln(N - S + 1)$

and $H'_{max} = \ln S$, and

7. an index of similarity of species composition (percent similarity) between pairs of samples, calculated by comparing the proportional abundances of each species occurring in both samples, taking the smaller, and summing.

Statistical analysis of the data was done on an IBM 360 computer using APL. Programs used were obtained from the public library of the University of Alberta computing center, and were based on procedures outlined in Steel and Torrie (1960) and Sokal and Rohlf (1969). Most data were analyzed by an analysis of variance for unequal sample sizes (Library 2, STP 2, ANOVA 2). Product-moment correlation coefficients were determined using Library 160, PSTAT, CORR. Stepwise multiple regression formulae were determined using Library 2, STP 2, STREG. In addition, frequencies of concurrent infections were analyzed using the G-statistic (Sokal and Rohlf, 1969) and a hand calculator.

IV. THE COMMUNITY OF PARASITES

A total of 3,105 fish, belonging to ten species from six families, were examined for parasites (Table 3). The family Salmonidae was represented by four species, other families by only one or two species. The species with the highest numbers of individual fish examined were ninespine sticklebacks, whitefish and cisco, with walleye and longnose sucker having the least.

Thirty-seven species of parasites were recovered; they belong to the Monogenea (2 spp.), Trematoda (7), Cestoda (14), Nematoda (5), Acanthocephala (3), Annelida (1) and Copepoda (5). *Metechinorhynchus salmonis*, which matured in six fish species, was the most common parasite recovered; other parasites commonly recovered were *Ergasilus auritus*, *Ergasilus nerkae*, *Cyathocephalus truncatus* and *Proteocephalus* plerocercoids. ("*Proteocephalus* plerocercoids" is probably an artificial assemblage of immature stages of several species. All were in the intestine; all lacked mature proglottids or any other distinctive character.)

Each of the species of fishes examined had a characteristic assemblage of species of parasites. These assemblages (= communities) differed in many respects (Table 4). The number of species (S) was highest in whitefish (16) and lowest in walleye (3); the mean number of species per infected fish ($\bar{S}$) varied from a high of 4.6 in whitefish to a low of 1.83 in whitesuckers. A particularly large proportion of the species of parasites in sticklebacks were in the larval stages. The mean number of individual parasites per infected host ($\bar{N}$) was largest in lake

Table 3. The species of parasites recovered from ten species of fishes in Cold Lake, Alberta

	Salmonidae				Esocidae	Catostomidae		Gadidae	Gasterosteidae	Percidae
	Whitefish	Cisco	Lake Trout	Coho	Northern Pike	Whitesucker	Longnose Sucker	Burbot	Stickleback	Walleye
No. Exam.	836	757	35	288	62	36	12	29	[illegible]	[illegible]
Monogenea										
Discocotyle sagittata (Leuckart, 1842)	65.3 (4.3)[a] (1-58)	20.9 (2.1) (1-12)		0.3 (1) (1)						
Gyrodactylus sp.									59.5[1]	
Trematoda										
**Apatemon gracilis* (Rud. 1819)									11.0 (2.8) (1-4)	
Bunodera luciopercae (Müller, 1776)									4.3 (2.8) (1-16)	
**Cotylurus erraticus* (Rud., 1809)	48.7[1]	1.1[1]							45.6[1]	
Crepidostomum farionis (Müller, 1784)	0.2 (1) (1)	1.6 (1.7) (1-12)		7.3 (2.1) (1-10)						
**Diplostomum Spathaceum* (Rud., 1819)	1.4 (1) (1)		5.7 (1) (1)						[illegible] 4.6 [illegible]	
Lissorchis attenuatum Van Cleave and Mueller, 1932						13.8 (2.4) (1-21)				
Phyllodistomum coregoni Dechtiar, 1966	1.9 (2.9) (1-11)									
Cestoda										
Bothriocephalus cuspidatus Cooper, 1917										75 (9.9) (3-2[illegible])
Caryophyllaeus sp.						5.6 (2.5) (2-3)	50 (7.7) (2-13)			
Cyathocephalus truncatus (Pallas, 1781)	72.8 (28.2)	7.8 (3.5) (1-43)		0.7 (1) (1)				6.9 (3) (2-4)		
**Diphyllobothrium* sp.	0.1 (1) (1)	1.2 (1.7) (1-10)		4.9 (1.4) (1-3)						
Eubothrium rugosum (Batsch, 1786)								79.3 (12.8) (1-128)		
Eubothrium salvelini (Schrank, 1790)			100 (33.3) (1-87)							
***Eubothrium* spp.				1.7 (4.2) (1-5)					4.4 (1.2) (1-4)	
Hunterella sp.						5.6 (1.5) (1-2)				
Proteocephalus exiguus LaRue, 1911	14.3 (12.7)									
Proteocephalus filicollis Rud., 1802		20.3 (13.2) (1-100)							11.7 (1.8) (1-11)	
Proteocephalus pinguis LaRue, 1911					1.6 (21) (21)					
***Proteocephalus* sp. (A)										50 (9.2) (3-23)
***Proteocephalus* spp.	12.8 (18.1)	53.1 (27.4) (1-850)		3.1 (9.8) (1-27)	66.1 (61.1) 1-723					
**Schistocephalus solidus* (Müller, 1776)					1.6 (2) (2)				31.6 (1.1) (1-3)	
Triaenophorus crassus (Forel, 1868)					3.2 (1.5) (1-2)					
**T. crassus*		0.7 (1.2) (1-2)								
Triaenophorus nodulosus (Pallas, 1760)					90.3 (35.2) (1-752)			6.4 (4) (4)	11.8 (1.4) (1-5)	
**T. nodulosus*			5.7 (1) (1)	2.8 (1.4) (1-2)						

Table 1. Continued:

	Salmonidae				Esocidae	Catostomidae		Gadidae	Gasterosteidae	Percidae
	Whitefish	Cisco	Lake Trout	Coho	Northern Pike	Whitesucker	Longnose Sucker	Burbot	Stickleback	Walleye
No. Exam.	836	757	35	288	62	36	12	29	1038	12
Nematoda										
Cystidicola stigmatura (Leidy, 1886)	76.1 (12.6) (1-85)			4.2 (3.1) (1-8)						
***C. stigmatura*		1.9 (2.5) (1-11)								
Haplonema sp.								51.7 (5.5) (1-20)		
Philonema agubernaculum Simon and Simon, 1936		0.9 (6.3) (2-11)		15.3 (19.3) (1-130)						
Raphidascaris sp.					3.2 (1.5) (1-2)					
**Raphidascaris* sp.			8.6 (1.7) (1-3)							
Rhabdochona cascadilla Wigdor, 1918						8.3 (1.3) (1-2)	58.3 (10.3) (1-25)		0.2 (1) (1)	
Acanthocephala										
Metechinorhynchus salmonis (Müller, 1784)	99.5 (170) (1-1340)	32.4 (8.7) (1-76)	100 (421) (92-934)	99.2 (162) (1-1549)	83.9 (30.5) (1-226)			100 (174) (38-537)		
***M. salmonis*										
Neoechinorhynchus strigosum Van Cleave, 1949						8.3 (4) (1-7)	83.3 (30.9) (2-75)		19 (1.8) (1-8)	66.7 (3) (1-4)
***N. strigosum*						13.8 (2.4) (1-5)				
Pomphorhynchus bulbocolli (Linkins, 1919)				0.7 (3) (3)	1.6 (4) (4)	100 (37.9) (5-124)				
***P. bulbocolli*	1.0 (2) (1-12)	2.0 (2.5) (1-8)	5.7 (1) (1)	5.9 (1.7) (1-10)					0.6 (1.5) (1-2)	
Annelida										
Cystobranchus verrilli [1]Meyer, 1940								3.4 (6) (6)		
Copepoda										
Ergasilus auritus (Markevich, 1940)	1.2 (21.4) (1-16)	25.1 (12) (1-155)	5.7 (126) (4-247)	16.7 (6.4) (1-40)					13.3 (2.1) (1-5)	
Ergasilus nerkae Roberts, 1963	5.1 (14.2) (1-95)	35.3 (13.2) (1-173)	2.9 (1) (1)	37.8 (28.7) (1-103)						
Ergasilus sp.						11.1 (2.5) (1-4)	11.1 (11) (11)			
Salmincola extensus (Kessler, 1868)	30.9 (1.9) (1-7)	0.1 (1) (1)								
Salmincola extumescens (Gadd, 1901)	26.3 (1.6) 1-4									

*Larval

**Immature

[1] Number of individuals not counted

[a] Prevalence (mean intensity)
Range

Table 4. Diversity of the parasite faunas of fishes from Cold Lake, Alberta

	No. examined (n)	No. infected (I)	No. spp. (S)	Mean no. spp. per infected fish ($\bar{S}$)	No. spp. mature (SM)	Mean no. individuals per infected fish ($\bar{N}$)	Simpson's Index (SI)	Shannon-Weaver Index (H')	Evenness (E)
Stickleback	1038	923	13	3.24	4	14.06	3.78	1.60	0.61
Cisco	757	670	15	2.47	9	32.69	3.24	1.52	0.55
Pike	62	62	8	2.53	5	89.94	2.75	1.08	0.52
Walleye	12	11	3	2.09	2	15.27	2.45	0.98	0.89
Longnose sucker	12	12	4	2.00	3	36.50	1.90	0.90	0.64
Whitefish	836	828	16	4.60	11	211.60	1.55	0.83	0.30
Coho	288	286	14	2.02	8	178.09	1.20	0.39	0.15
Trout	35	35	8	3.6	4	504.66	1.19	0.34	0.16
Burbot	29	29	6	3.42	5	228.96	1.16	0.31	0.17
Whitesucker	36	36	8	1.83	7	38.06	1.09	0.24	0.11

trout (505) and lowest in sticklebacks (14) and walleye (15). Diversity, as measured by Shannon-Weaver's H', Simpson's Index (SI) or Hurlburt's measure of evenness (E), varies considerably between species of fish, with particularly low values (SI less than 1.6, E less than 0.4) in five fishes (whitefish, trout, coho, whitesucker and burbot). The parasite faunas in all these hosts were dominated by acanthocephalans, *Pomphorhynchus bulbocolli* in whitesucker and *M. salmonis* in the others.

Two of these measures of the communities of parasites appear to be reflections of the number of fish examined (n). Both S and H' were significantly correlated with n (Table 5), suggesting that more rare species were recovered with an increase in n. This is further strengthened by the lack of a statistically significant correlation between n and SI ($t = 2.09$, $P > 0.05$), which is less sensitive to rare species than H'.

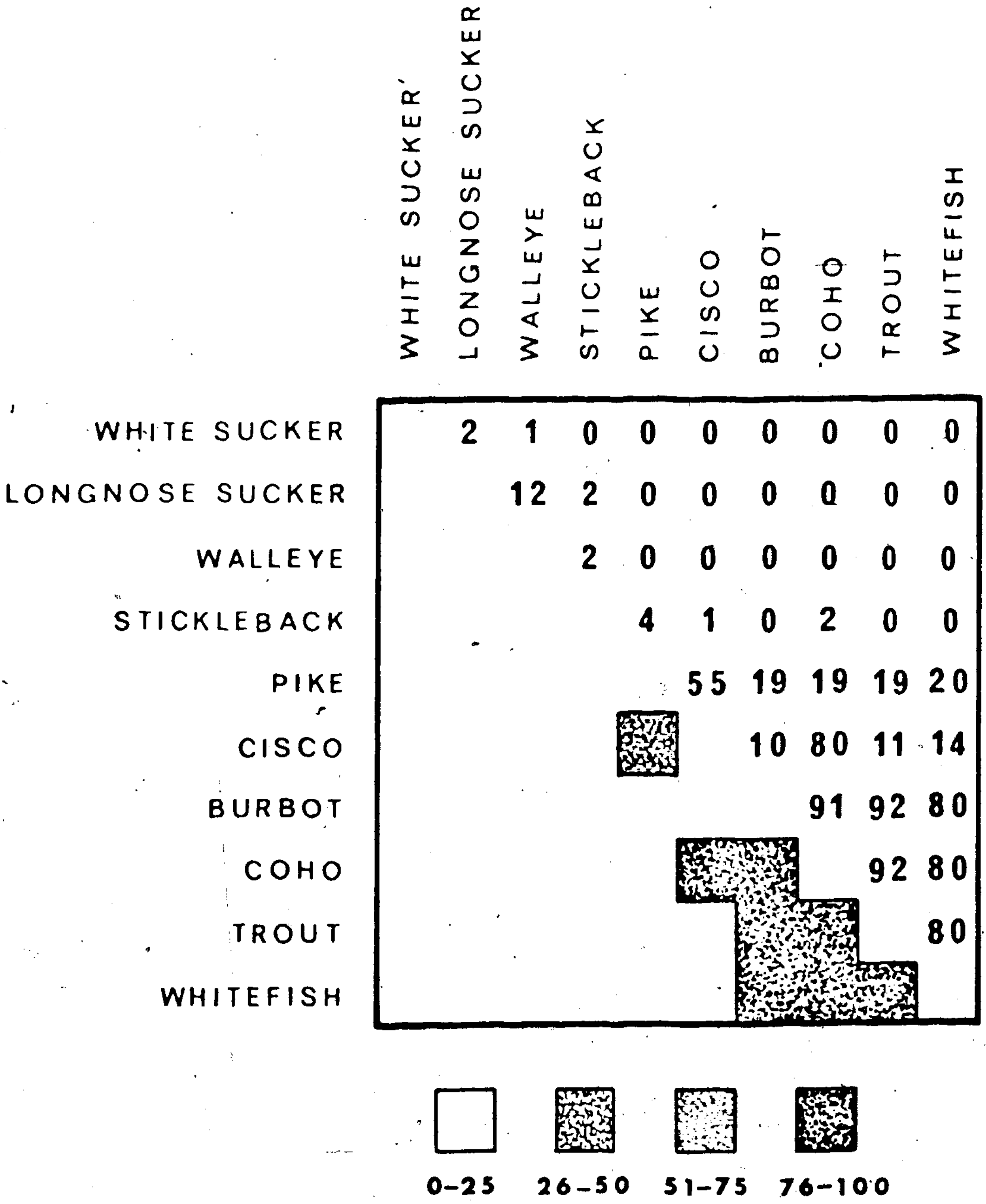
The three measures of diversity are obviously closely correlated (Table 5), making presentation of more than one redundant in most cases. Since SI has the widest range of values, it seems to show relationships best, and will be used in the rest of this thesis. The other two will be discussed only when they show different patterns.

When the species composition of the parasite communities in various fish hosts are compared by means of the percent similarity method, a single cluster was apparent (Figure 3). This cluster had a central group consisting of burbot and three salmonids (whitefish, trout and coho), characterized by high similarities between their parasite communities, and by high abundances of *M. salmonis*. The fourth salmonid (cisco) showed high similarities to coho (both had high abundances of the two species of *Ergasilus*), but not to the other three. The only

Table 5. Correlations between various measures of diversity of the parasite faunas of different fish hosts. Correlation coefficients within boxes are statistically significant ($P < 0.05$).

	n	S	$\bar{S}$	SM	$\bar{N}$	H'	SI
S	$\boxed{.80}$						
$\bar{S}$	.48	.42					
SM	.50	$\boxed{.83}$	.34				
$\bar{N}$	.06	.57	.41	.07			
H'	$\boxed{.68}$	.30	-.02	.04	-.58		
SI	.59	.21	-.07	.17	.22	$\boxed{.97}$	
E	.16	.29	-.26	.48	-.57	$\boxed{.76}$	$\boxed{.74}$

Figure 3. Percent similarity between parasite communities in fishes from Cold Lake, Alberta



	WHITE SUCKER	LONGNOSE SUCKER	WALLEYE	STICKLEBACK	PIKE	CISCO	BURBOT	COHO	TROUT	WHITEFISH
WHITE SUCKER		2	1	0	0	0	0	0	0	0
LONGNOSE SUCKER			12	2	0	0	0	0	0	0
WALLEYE				2	0	0	0	0	0	0
STICKLEBACK					4	1	0	2	0	0
PIKE						55	19	19	19	20
CISCO							10	80	11	14
BURBOT								91	92	80
COHO									92	80
TROUT										80
WHITEFISH										

other high similarity, between cisco and pike, may be misleading, since it is largely due to high abundance of *Proteocephalus* plerocercoids, which actually may be different species in the two hosts. Most of the other fishes are characterized by parasites specific to them.

The importance of each host fish in the community of fishes (as determined by the relative abundance = weighting factor, p. 16), and the importance of each species of parasite in each of those fish (as determined by the relative abundance of each parasite, Appendix I) are illustrated in Figure 4. For example, cisco was the most abundant fish, with a weighting factor of 100 (or 51.8%) out of a total of all weighting factors of 193.48; its slice of the pie in Figure 4 was therefore 51.8%, or 186°. The most abundant parasite in cisco, *Proteocephalus* plerocercoids, made up 50.3% of the total parasite abundance in cisco; its slice of the cisco slice was therefore 93°.

It [illegible] obvious from Figure 4 that the salmonids, mainly whitefish and [illegible] dominated the community of fishes. It is also obvious that *M. s*[illegible]kes up a substantial portion of the community of parasites in al[illegible]ery species of fish.

[illegible] mean number of parasites per infected fish varied greatly between fish species; therefore, one cannot get a good idea of the relative abundance of each species of parasite by examining Figure 4. Therefore, the weighted dominance index, which is a measure of the relative abundance in the total community of parasites, was calculated (p. 15) for each species. The results are shown in Figure 5. It is apparent that parasites typical of salmonids, especially *M. salmonis*, dominated the community of parasites.

Within this community of parasites, a large proportion of the

Figure 4. The dominant parasites in each species of fish host in Cold Lake, Alberta

Gyro - *Gyrodactylus* sp., Ag - *Apatemon gracilus*,
Ce - *Cotylurus erraticus*
Dsp - *Diplostomum spathaceum*
Both - *Bothriocephalus cuspidatus*
Cary - *Caryophullaeus* sp.
Ct - *Cyathocephalus truncatus*
Pf - *Proteocephalus filicollis*
Pp - *Proteocephalus* plerocercoids
Prot - *Proteocephalus* sp. (A)
Ss - *Schistocephalus solidus*
Tn - *Triaenophorus nodulosus*
Cs - *Cystidicola stigmatura*
Rhab - *Rhabdochona cascadilla*
Ms - *Metechinorhynchus salmonis*
Pomp - *Pomphorhynchus bulbocolli*
Ea - *Ergasilus auritus*
En - *Ergasilus nerkae*

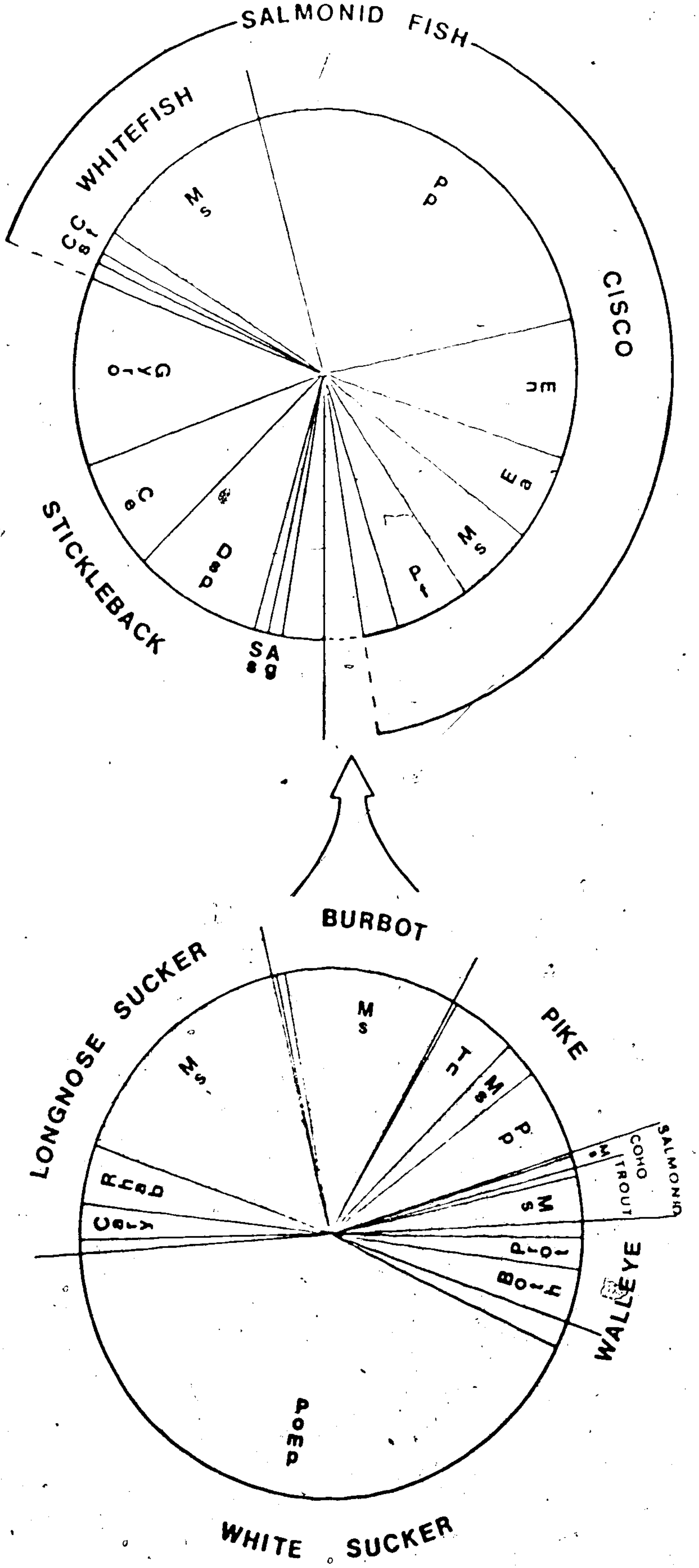
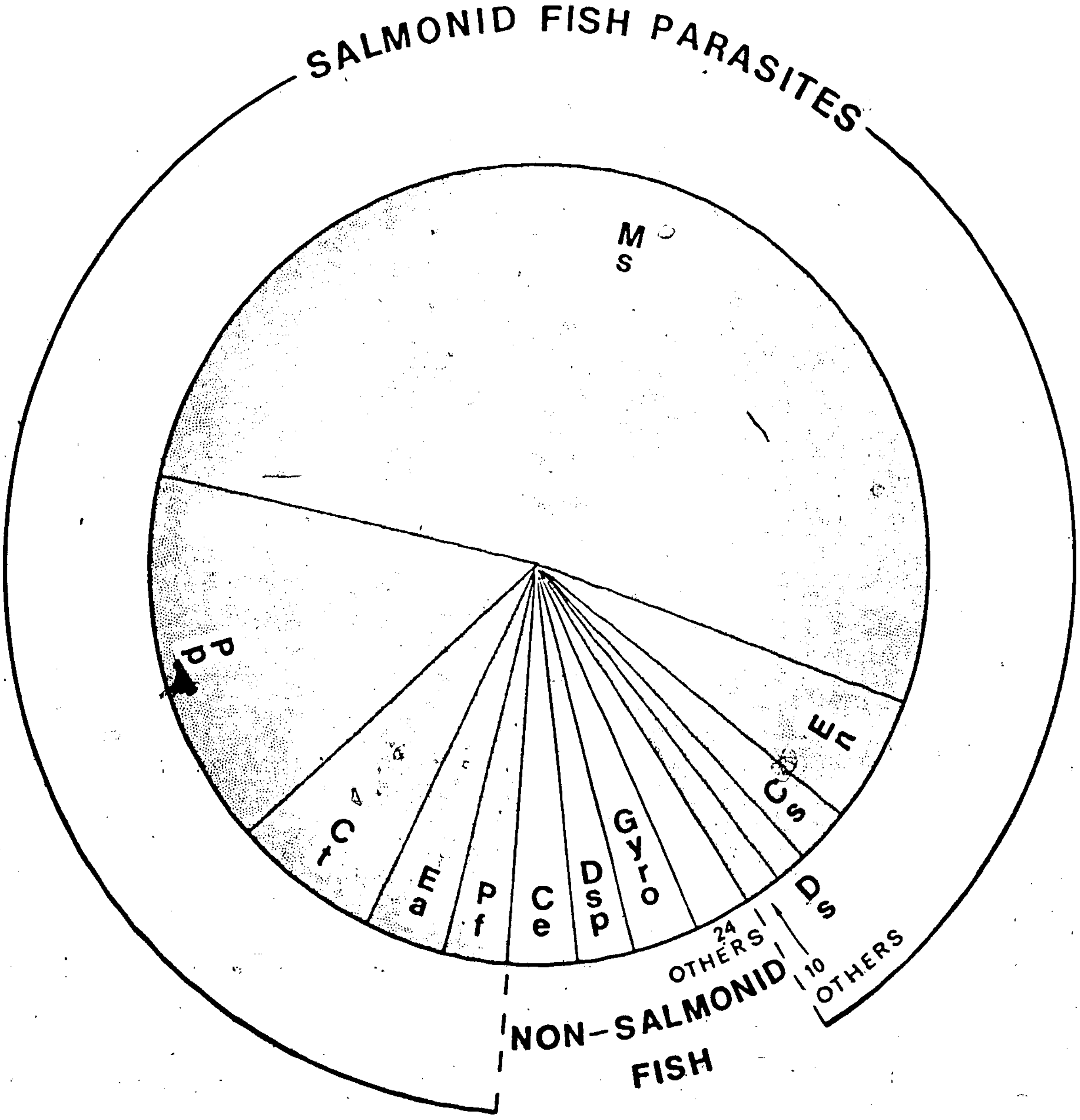

SALMONID FISH
WHITEFISH
CISCO
STICKLEBACK
Pp
Ms
Cc
Gyo
Eu
Ea
Ms
Pf
Dp
Ce
SA
BURBOT
LONGNOSE SUCKER
PIKE
SALMONID
COHO
TROUT
WALLEYE
WHITE SUCKER
Ms
Ms
Tu
Ms
Pp
Ms
Pio
Bot
Rhea
Cary
Poep

Figure 5. The dominant parasites of a community of fishes in Cold Lake, Alberta. The portion of each section of the pie represents the dominance of each species of parasite within the community.

Ds - *Discocotyle sagittata*
Gyro - *Gyrodactylus* sp.
Ce - *Cotylurus erraticus*
Dsp - *Diplostomum spathaceum*
Ct - *Cyathocephalus truncatus*
Pf - *Proteocephalus filicollis*
Pp - *Proteocephalus* plerocercoids
Cs - *Cystidicola stigmatura*
Ms - *Metechinorhynchus salmonis*
Ea - *Ergasilus auritus*
En - *Ergasilus nerkae*


SALMONID FISH PARASITES
Ms
Pp
Ct
Ea
Pf
Ce
Dsp
Gyro
Cs
En
Ds
24 OTHERS
10 OTHERS
NON-SALMONID FISH

species (70%) matured in one or more of the fish hosts (Table 6). Cestodes had the most species of hosts (12), but they had a fairly low total dominance index (9.8). Only three species of acanthocephalans were recovered, but they had the highest total dominance index (53). Only 30% of the species of parasites recovered were larval forms, of which most (19%) matured in fish (Table 6).

DISCUSSION

In Cold Lake, the number of species of non-salmonid fishes is greater than that of salmonids (Paetz and Zelt, 1974; Roberts, 1975), a situation similar to that in other oligotrophic lakes in which the parasites have been studied (Bangham and Hunter, 1939; Bangham, 1955; Dechtiar, 1972). In all cases, the non-salmonid fishes have a greater number of species of parasites than the salmonid fishes (Table 7). Also shown in Table 7 are the results of two surveys of eutrophic lakes, Trumbull Lake, Iowa (Meyer, 1958), and Družno Lake, Poland (Wisniewski, 1958; Kozicka, 1958, 1959). In each of the last two, only non-salmonids were present.

In terms of abundance, the salmonids in Cold Lake, particularly the cisco and to a lesser extent the whitefish, dominated the community of fishes and the species of parasites typical of the dominant salmonids dominated the parasite community. This observation agrees with Wisniewski's (1958) general conclusion that the parasite community within an ecosystem is characterized by parasites of the dominant hosts. Chubb (1963a) came to a similar conclusion. Unfortunately, none of the studies summarized in Table 7 provided data on intensity of infection, or on relative

Table 6. A comparison between the number of species and their abundance for larval parasites and adult parasites belonging to different major classes in Cold Lake, Alberta

	Sum of dominance indices	No. spp.	Percent of total
Adult parasites	78.44	32	70
Monogeneans	4.1	2	4
Trematodes	0.12	4	9
Cestodes	9.8	12	26
Nematodes	2.87	5	11
Acanthocephalans	53.14	3	7
Others	8.41	6	13
Larval stages	21.56	14	30
To fish	16.07	9	19
To birds	5.49	5	11

Table 7. The number of species in major groups of parasites recovered from salmonid and non-salmonid fish in various lakes

	Cold [illegible]ake		Lake of The Woods		Lake Huron		Lake Erie		Trumbull Lake	Drużno Lake
	S* 1916(4)**	NS 1189(6)	S 74(3)	NS 585(38)	S 294(8)	NS 1373(45)	S 181(4)	NS 3087(76)	NS 1672(13)	NS 1388(21)
Adults	14	21	18	111	17	60	7	153	19	35
Monogenea	1	1	1	32	1	5	0	50	5	4
Trematoda	2	2	2	26	2	17	0	37	6	12
Cestodes	4	10	5	14	3	13	3	22	6	7
Nematodes	2	3	3	8	2	8	1	15	1	3
Acanthocephalans	1	3	3	13	3	8	2	12	1	4
Others	4	2	4	18	6	9	1	17	0	5
Larval stages	11	10	4	31	8	21	2	39	8	21
To birds	3	4	3	18	3	9	2	19	7	15
To fish	8	6	1	13	5	12	0	20	1	6

*S - Salmonid fish; NS - Non-salmonid fish.

**No. of fish examined (no. of fish species examined).

proportions of the different host species, so that Wisniewski's conclusion cannot be tested with their data.

Wisniewski (1958) also concluded that in eutrophic ecosystems, most of the larval parasites in fish culminated their life cycle in piscivorous birds or mammals. Esch (1971) agrees with Wisniewski's specific conclusion and proposed a trophic-level hypothesis of predator-prey relationships to explain such differences in parasite distribution. Esch *et al.* (1975) expanded that hypothesis, pointing out that oligotrophic systems are relatively closed, with negligible aquatic-terrestrial interactions, whereas eutrophic ecosystems are more open, with extensive aquatic-terrestrial interactions.

These conclusions can be tested, using the data from the studies summarized in Table 7. Drużno and Trumbull Lakes show the ratios of larval forms completing their life cycles in birds to those completing their life cycles in fish that were predicted for eutrophic lakes. Cold Lake and Lake Huron show ratios predicted for oligotrophic lakes. However, Lake of the Woods, an oligotrophic lake on the Canadian Shield, has a high proportion of larval parasites completing their life cycles in piscivorous birds, and the much more eutrophic Lake Erie has a relatively high proportion maturing in fish (or at least, did in the 1939 survey). These last two surveys indicate different predator-prey relationships and aquatic-terrestrial interactions than would be predicted on the basis of degree of eutrophication.

In order to compare the parasite communities of the species of fishes collected at Cold Lake with those of the same species collected elsewhere, I recalculated Simpson's Index for each, using data on prevalence only. I also calculated Simpson's Index for the same species in other surveys (Table 8). (These indices are not as satisfactory as those using data on abundance, but the required data on intensity were not available.)

In general, the diversity in Cold Lake was among the lowest for each species. Whitefish may be an exception, with the diversity in Cold Lake somewhat higher than that in Lake Huron or coastal Labrador, but somewhat lower than that in Lake of the Woods. It should be noted that the diversities calculated in this way for the parasites of fishes of Cold Lake, although low, are considerably higher than those calculated using data on abundance (Table 4). The latter reflect the general dominance of the communities by high numbers of acanthocephalans, *P. bulbocolli* in whitesucker and particularly *M. salmonis* in other species. The unusual dominance in so many species of fish hosts by *M. salmonis* will be discussed in section VII.

Table 8. Simpson's indices, based on prevalence, of the parasite faunas of various species of fish in different lakes in North America

	CL*	LW	TL	LH	LE	LAB
Whitefish	7.04	9.23	-	5.18	-	3.39
Cisco	6.92	15.16	-	5.49	-	-
Lake trout	2.72	7.30	-	3.05	-	12.12
Pike	3.19	9.75	3.98	6.72	4.58	-
Whitesucker	2.48	12.26	2.46	5.56	-	-
Burbot	3.20	13.11	-	5.09	-	-
Walleye	2.92	14.75	-	3.01	2.71	-

*CL - Cold Lake; LW - Lake of the Woods, Ontario; TL - Trumbull Lake, Iowa; LH - Lake Huron; LE - Lake Erie; LAB - Coastal Labrador.

V. MODIFYING FACTORS

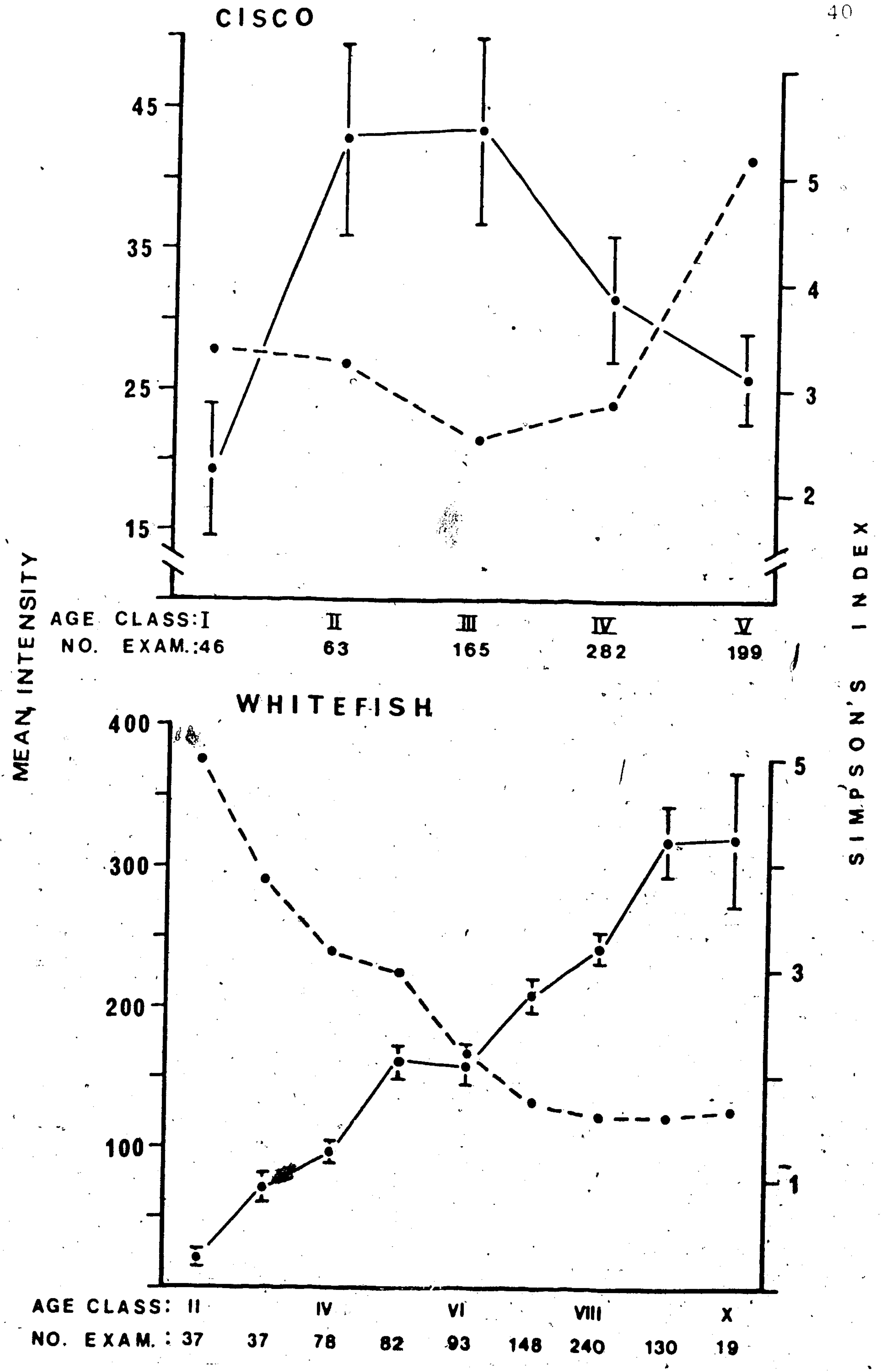
A. FISH AGE

Enough individuals belonging to different age classes of whitefish, cisco and coho were examined so that data from these three fishes could be used to determine the effects of age of the fish on their parasite communities.

The patterns of these communities are shown best in the data from whitefish (9 age classes) and cisco (5 age classes). The patterns of $\bar{N}$ and SI are shown in Figure 6. Details, and data on measures not shown in the Figures, are provided in Appendices II and III. In both species of fish, S increased slowly with age, then declined in the oldest age class. Unfortunately, sample sizes followed the same pattern, so it is not clear whether the basic relationship is an increase in species of parasite with age or with sample size. Except for a lower value in the youngest age class of whitefish, $\bar{S}$ did not differ significantly among age classes in either species.

The patterns of other measures were markedly different between the two species of fish. In whitefish, $\bar{N}$ increased in a roughly linear fashion with age, but in cisco, there was no significant variation in $\bar{N}$ with age. In whitefish, SI, H' and E were all decreasing, concave functions of age (exemplified by SI in Figure 6), with H' somewhat more flattened than the others. In cisco, SI and E decreased with age to minimal values in age classes III and IV, then increased; H' was essentially constant in age classes I through IV, then increased.

Figure 6. The mean intensity (± Standard Error) (————) and Simpson's Indices (--------) of whitefish age classes II to X and of cisco age classes I to V


CISCO
45
35
25
15
5
4
3
2
AGE CLASS: I
II
III
IV
V
NO. EXAM.: 46
63
165
282
199
MEAN INTENSITY
SIMPSON'S INDEX
WHITEFISH
400
300
200
100
5
3
1
AGE CLASS: II
IV
VI
VIII
X
NO. EXAM.: 37
37
78
82
93
148
240
130
19

The two available age classes of coho were examined; S, $\bar{S}$ and $\bar{N}$ were signif[illegible] higher in the older fish, even though the sample size was smalle[illegible]r diversity indices (SI, H' and E) were smaller in the older f[illegible]9).

[illegible]ndiv[illegible]ecies of parasites show various patterns of abundance with [illegible] Do[illegible] (1961) followed Gorbunova (1936) in recognizing thr[illegible] patter[illegible] a[illegible]dance independent of age, an increasing function of age (the us[illegible]e), and a decreasing function of age. An additional pattern [illegible]e apparent in the present study: abundance reaching a maximum v[illegible]e in middle age. The patterns shown by the common parasites of whitef[illegible] cisco and coho are summarized in Table 10.

Only[illegible]e species (*E. nerkae*) showed a decrease in abundance with age; this decrease was consistent in all three fishes. Only one of the relatively abundant species (*Diphyllobothrium* plerocercoids in cisco) was apparentl[illegible]dependent of age. The rest of the abundant species increased w[illegible]ge, or reached maximal abundances in middle-aged fish. Except for the impossibility of detecting the last pattern in coho, and for *D. sagittata*, which reached maximum abundances in age classes IV and V in whitefish, but increased through all age classes in cisco, the patterns shown by individual parasites in different fishes were consistent.

In whitefish and coho the patterns of the most common parasites (including the dominant *C. truncatus*, *C. stigmatura* and *M. salmonis*) showed an increase in abundance with age, but in cisco, the majority of the most common parasites (including the dominant *Proteocephalus* plerocercoids) reached a maximum at middle age.

The abundances of several parasites, notably *D. sagittata*, *P. exiguus*, *Proteocephalus* plerocercoids and *C. stigmatura* between age

Table 9. The diversity of the parasite community in coho age classes II and III

		Age class	
		II	III
No. examined	(n)	210	78
No. species	(S)	10	13
Mean no. species ± S.E.	($\bar{S}$)	1.80 ±0.06	2.68 ±0.17
Mean no. individuals ± S.E.	($\bar{N}$)	70.0 ±4.79	555.8 ±44.4
Simpson's Index	(SI)	1.46	1.10
Shannon-Weaver Index	(H')	0.58	0.26
Evenness	(E)	0.25	0.10

Table 10. The patterns of abundance with age of the most common parasites of whitefish, cisco and coho

Patterns	Whitefish	Cisco	Coho
Independent		*Diphyllobothrium* sp.**	
Increase	*Cotylurus erraticus*** *Cyathocephalus truncatus* *Cystidicola stigmatura* *Metechinorhynchus salmonis* *Salmincola extumescens*	*Discocotyle sagittata* *Cyathocephalus truncatus* *Philonema agubernaculum* *Metechinorhynchus salmonis*	*Crepidistomum farionis* *Cystidicola stigmatura* *Philonema agubernaculum* *Metechinorhynchus salmonis* *Ergasilus auritus*
Decrease	*Ergasilus nerkae*	*Ergasilus nerkae*	*Ergasilus nerkae*
Maximum in middle age	*Discocotyle sagittata* *Proteocephalus exiguus* *Proteocephalus* spp.* *Salmincola extensus*	*Crepidistomum farionis* *Proteocephalus filicollis* *Proteocephalus* spp.* *Pomphorhynchus bulbocolli** *Ergasilus auritus*	

*Immature form.

**Larval form.

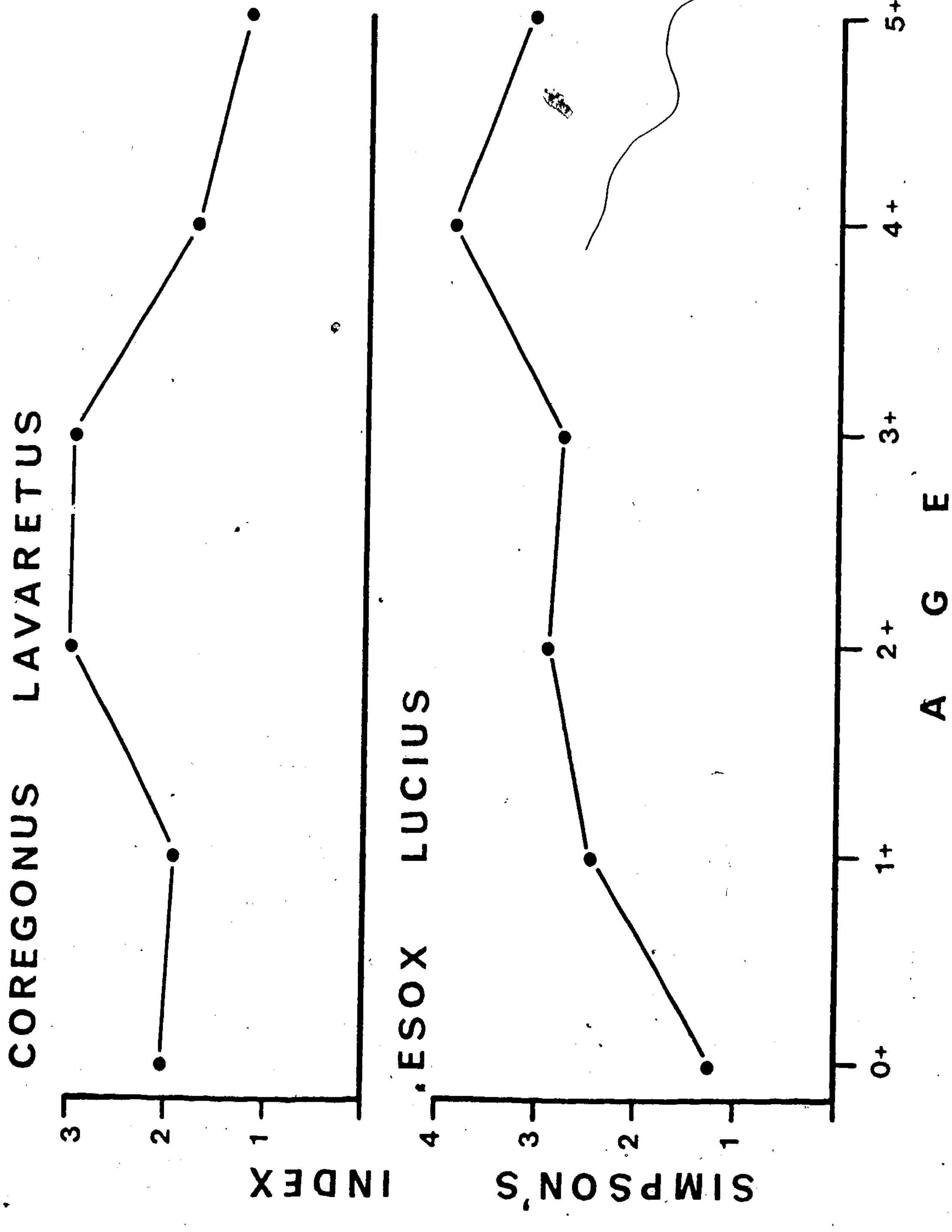
classes VI and VII in whitefish and *Proteocephalus* plerocercoids between age classes III and IV in cisco, showed an obvious break just prior to the prime reproductive years of each host (Appendices II and III).

Discussion

In his monumental review of the ecology of parasites of freshwater fishes, Dogiel (1961) concluded that parasite communities in fishes increase in complexity ("become more variable") with age. He used $\bar{S}$ as an index of complexity, and cited data from a number of fishes, including *Coregonus lavaretus* and *Esox lucius*, which agree with the hypothesis. Dogiel pointed out that data (from Layman, 1946) on parasites of cultured carp are an exception, showing no change in $\bar{S}$ with age. He attributed this difference to the confined environment of the cultured fish. However, he also cited data from Dubinin (1936) on parasites of *Thymallus thymallus* which showed an increase in $\bar{S}$ between the 0+ and 1 year-old fish, but no further increase in fish up to 4 years old. My data on $\bar{S}$ in whitefish show essentially the same pattern as that for *Thymallus*, with no further increase after age class III. No 0+ cisco were examined in this study, but $\bar{S}$ showed no significant variation in ciscos between age classes I and V. In coho, $\bar{S}$ did increase between age classes, agreeing with Dogiel's hypothesis.

Dogiel provides data on only two species, *Coregonus lavaretus* and *Esox lucius*, for which an index of diversity can be calculated and used as a measure of complexity. In *E. lucius*, SI did generally increase with age, agreeing with his conclusion, but in *C. lavaretus*, SI did not continue to increase with age, but reached a maximum at ages 2+ and 3+, then declined (Figure 7).

Figure 7. Simpson's Indices for *Coregonus lavaretus* and *Esox lucius* of age classes 0+ to 5+ (data from Dogiel, 1961)


COREGONUS LAVARETUS
ESOX LUCIUS
SIMPSON'S INDEX
3
2
1
4
3
2
1
AGE
0+
1+
2+
3+
4+
5+

In my data on whitefish and coho, SI showed a consistent decrease in complexity with age, but in my data on cisco, SI reached maximal levels in middle-aged fish. These patterns of diversity showed inverse relationships with the patterns of abundance of the dominant parasites in each host, which were directly responsible for setting the patterns of $\bar{N}$. These inverse relationships are apparently due to the acquisition of disproportionally large numbers of the dominant parasites, particularly *M. salmonis* in whitefish and coho and *Proteocephalus* plerocercoids in cisco, as the host aged.

It appears that the relationship between complexity of the parasite community and age of the host may depend on the ecosystem from which the host is taken and that general rules, such as Dogiel's, may not work in some systems.

Dogiel (1961, 1964) pointed out that changes in infection with age of the host might be due to an increased surface area (for ectoparasites), a change in amount and type of food consumed, the ability of some parasites to accumulate, or a change in the behaviour of the host. In addition, Schad (1966) has suggested that the immune system might be sensitized by one species of parasite, but operative against others.

Other authors have pointed out that individual species may be affected differently by the age of the host and that the effect of age on the same species of parasite may be different in different hosts, or in the same host in different locations, suggesting that effects (in some cases, at least) are functions of the ecosystem, not the host-parasite relationship *per se*.

Thomas (1964), examining *Salmo trutta*, and Chappell (1969b), working on *Gasterosteus aculeatus* in Yorkshire, found that the abundance of *Neoechinorhynchus rutili* decreased with age. Bibby (1972) and Walkey (1967) found that the same acanthocephalan, in *Phoxinus phoxinus* and *G. aculeatus* (in Durham), respectively, increased in abundance with age. Walkey showed that the increase in abundance was due to an increased consumption of the ostracod intermediate hosts as the host aged. Thomas attributed the decrease to a scarcity of the intermediate host, while Chappell attributed the decrease to a change in host diet and behaviour.

Awachie (1966b) found that the intensity of *C. truncatus* in *S. trutta* decreased with host age. However, Bauer and Nikolskaya (1957; in Dogiel, 1964) found that, in Lake Ladoga, only 4+ or older whitefish, *Coregonus lavaretus*, were infected. In both cases the authors attributed these changes to ecological factors, mainly a change in diet.

In the present study, the intensities of *C. truncatus* in whitefish and cisco showed a similar pattern of increase with age. The increase can be explained in part by diet (see section V, C). However, the increased size of the pyloric caeca in older fish may also be important. Halvorsen and Macdonald (1972) have shown that *C. truncatus* selects the more anterior, longer caeca in *S. trutta*. They suggest that the opening of the bile duct, beside the fourth caecum of the dorsal group, plays a part in the selectivity. I do not have quantitative data on the location of *C. truncatus* in the pyloric caeca, but my general observations agree with those of Halvorsen and Macdonald in that most *C. truncatus* in whitefish were distributed in the most anterior pyloric caeca, which are longer and also close to the opening of the bile duct. In the larger whitefish or cisco, these anterior caeca were larger, had larger openings, and each appeared to contain more tapeworms. The small size of the pyloric caeca of cisco may be one reason for the lower population density of *C. truncatus* in that host. In addition, the number of caeca in the anterior group may be important, as suggested by the much higher density of *C. truncatus* in whitefish, which have a much larger number of caeca in the anterior group, than in brown trout.

E. auritus, *E. nerkae* and various species of *Proteocephalus* appear to be primarily parasites of young fish. The ergasilids are ectoparasites which attach to the lateral margins of the gill filaments, with the second antennae wrapped around the filaments and the pointed claws thrusting into them (Kabata, 1970). With this method of attachment, the stronger gill-ventilating currents and/or the increased size of the gill filaments in older fish are unlikely to affect them, and are especially unlikely to affect the two species differently.

However, both species feed directly on the gill epithelium, like *Dactylogyrus* spp., which are known to stimulate a strong immune response from the host (Paperna, 1964). The ergasilids may also stimulate such an immunity. If so, the immune response may affect the two species differently (as it does with different species of *Dactylogyrus*; Paperna, 1964), possibly due to differences in the biology of the two species. The population of *E. nerkae* is highest in late summer, while that of *E. auritus* is highest in spring. The immune system may be more responsive at the higher summer temperatures than at the lower spring temperatures. Thus one could expect the immune response to be more effective against *E. nerkae* than *E. auritus*, which is what the age-specific patterns suggest.

An additional factor may be involved in the reduction in numbers of ergasilids with age in whitefish (but not in cisco). The young whitefish lead a partially pelagic life, like cisco, as evidenced by the recovery of large numbers from gill-nets set at mid-water for cisco. The nauplii of ergasilids have a tendency to move to the surface waters at night (Bauer, 1959); therefore, the young whitefish may be exposed to larger numbers of infective nauplii than are the more benthic older fish.

Proteocephalids have *Cyclops* as their intermediate hosts. Although no *Cyclops* or other planktonic copepods were recovered from whitefish of any age class, the great intensity of proteocephalids in young fish suggested that *Cyclops* must have been consumed, presumably accidentally, more frequently in young fish. This is reasonable, considering their more pelagic habits.

One of the interesting features of my data is the difference in the pattern of abundance of *D. sagittata* with age in whitefish and cisco. Thomas (1964) found that the intensity of *D. sagittata* in *S. trutta* increased with host age up through age class IV, the oldest examined, as in cisco in my study. Paling (1969), however, working on the same host, found the abundance of *D. sagittata* increased to a maximum in age class VI, then decreased through age class IX, a pattern similar to that I found in whitefish.

The decrease in abundance of *D. sagittata* in older whitefish may be due to a combination of factors, including 1) stronger gill-ventilating currents; 2) larger gill filaments, which may affect the adhesive mechanism; and 3) behavioural changes associated with aging in whitefish.

Paling (1969) has shown that most oncomiracidia of *D. sagittata* passively landed on the second and third gills, but most adult parasites were found on the first and second gills. These suggested that through post-contact migration the parasites were actively selecting attachment sites away from the strongest ventilating currents. Llewellyn and Owen (1960) have shown that *D. sagittata* attaches, and inclines its body, so as to offer less resistance to the gill-ventilating currents. These features suggest that the stronger currents in bigger fish may be important.

Llewellyn and Owen also showed that the size relationship between the clamps and the gill lamellae is important. In the present study, *D. sagittata* in whitefish were observed to reach considerably larger sizes than in cisco. Paling (1965) showed that the size reached by *D. sagittata* increased with age of brown trout. He rejected the idea that the size of the parasites was limited in some way by the size of the host, and ascribed the increased size range to continued growth of the parasites over a period of several years. However, Halvorsen (1969) has argued that the morphological variations in the posterior part of the body of *Diplozoon paradoxum* from roach, bream and hybrids were adaptive responses for attachment to the different hosts. Halvorsen's argument suggests that the alternative hypothesis, that the size (morphology) of the same parasite in various ages of the same host, or in different hosts, is modified to adapt to the environment, should be reconsidered. There may be a limit to the size of the gill lamella to which the parasites can adapt. Beyond that size, the adhesive mechanisms of the clamps may be less effective and strong gill-ventilating currents could have a greater chance of dislocating the parasite.

The physiological changes in whitefish associated with sexual maturation at age class VI could have effects on *D. sagittata*. However, the maturation of cisco at age class IV seemed to have no effect on

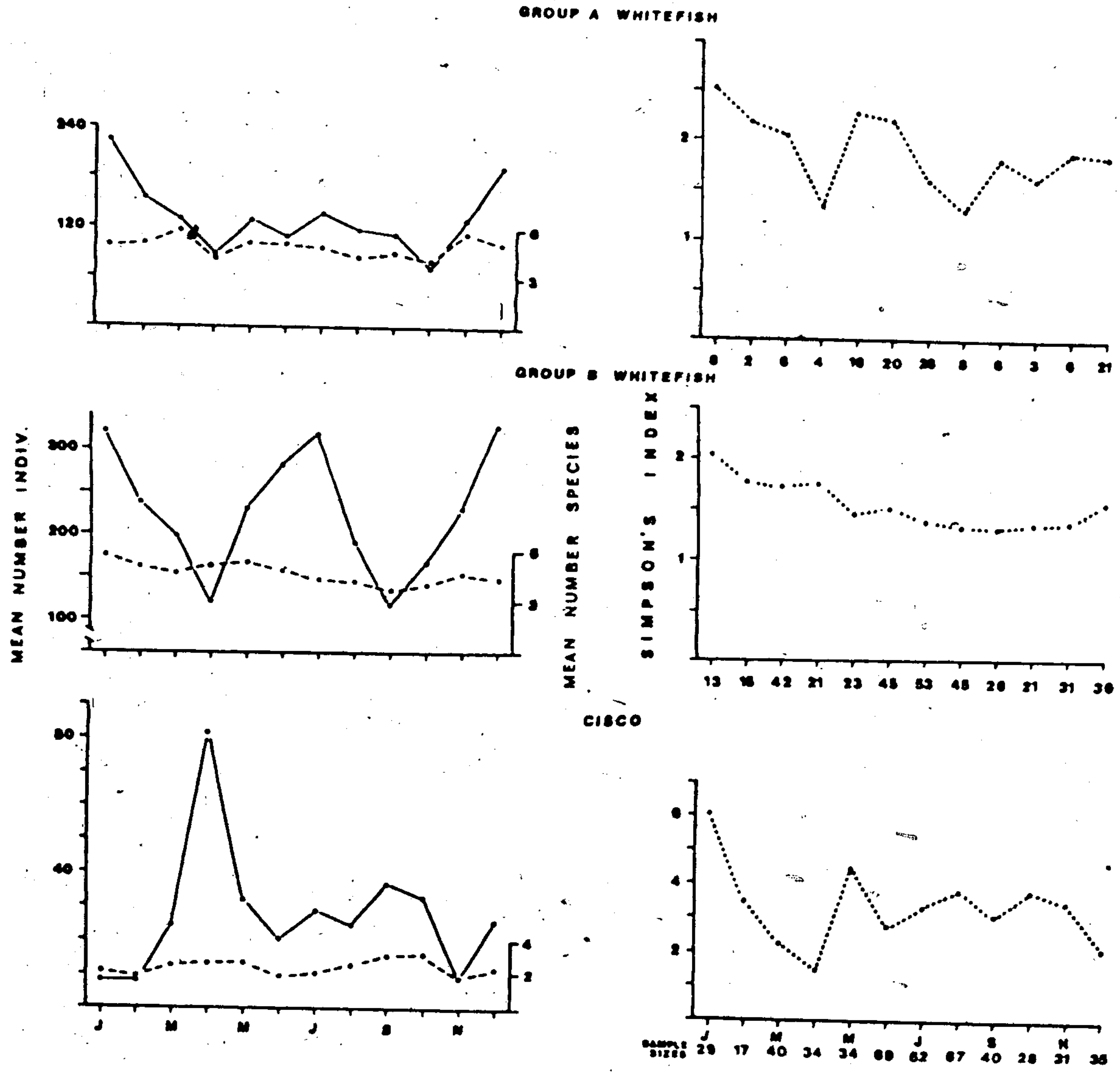
D. sagittata as the intensity continued to increase. Whitefish, but not cisco, show behavioural changes associated with aging; these changes, together with the behaviour of the infective larvae, may be important. The greater pelagic activity of the younger whitefish may result in greater contact with the infective oncomiracidia, since Paling (1969) showed that the oncomiracidia of *D. sagittata* swim to the surface in response to light.

B. SEASONS

Because of the significant effects of age of the hosts on their parasite communities, the effects of seasonal changes were examined within restricted groups of age classes. Two groups of whitefish were analysed: age classes IV and V (pre-reproductive classes, Group A), and age classes VII and VIII (prime reproductive classes, Group B). These two groups bracket the break in abundance of many species of parasites between age classes VI and VII. In addition, the overall $\bar{N}$ in Group B whitefish is nearly double that in Group A. If there are age-specific differences in seasonal patterns, these two groups should show them. Data on cisco consisted of those from age classes IV and V (prime reproductive classes).

The seasonal patterns of $\bar{S}$, $\bar{N}$ and SI of the parasite communities in the three groups of fish are shown in Figure 8. Details and data on other measures are given in Appendices IV to VI. In all three groups, S varied irregularly, with maximum values in the summer. $\bar{S}$ in both groups of whitefish decreased from early summer to late summer or early fall and fluctuated at a moderate level at other seasons. In cisco, $\bar{S}$ showed

Figure 8. Seasonal diversity (mean no. spp. ($\bar{S}$) (-------), mean no. individuals per infected fish ($\bar{N}$) (————), and Simpson's Indices (SI) (········)) of parasite communities in whitefish and cisco


GROUP A WHITEFISH
240
120
6
3
2
1
8 2 6 4 16 20 28 8 6 3 6 21
GROUP B WHITEFISH
MEAN NUMBER INDIV.
300
200
100
6
3
MEAN NUMBER SPECIES
SIMPSON'S INDEX
2
1
13 16 42 21 23 45 53 45 26 21 31 36
CISCO
80
40
4
2
J M M J S N
6
4
2
SAMPLE SIZES
J M M J S N
29 17 40 34 34 68 62 67 40 28 31 36

sharp decreases in early summer and mid-fall; each was followed by a gradual increase. The variation with season was statistically significant in Group B whitefish and cisco, but not in Group A whitefish, possibly because of small sample sizes.

Both Group B whitefish and cisco also showed significant changes in $\bar{N}$. Group B whitefish showed two peaks, in December and July, with minimum values in April and September. Although there was no statistically significant variation in $\bar{N}$ in Group A whitefish (again, probably due to the small sample sizes), the data did suggest a peak in winter. The patterns in cisco were the converse of that of Group B whitefish, with peaks in April and September, and minimum values in January-February and June.

In each of the three groups of fish, the three diversity indices (SI, H' and E) showed similar patterns. In Group A whitefish, diversity (as exemplified by SI in Figure 8) peaked in January and May, with minima in April and August. In Group B whitefish, diversity peaked in January, then decreased to a minimum in early fall. In cisco, diversity peaked in January, declined to a minimum in April, then increased to a fairly constant level through the rest of the year.

Parasite communities in all three groups showed a similar pattern of a maximum diversity in January, then a decrease to April, during the period of low, constant temperatures. This decreasing diversity accompanied a decreasing $\bar{N}$ in both groups of whitefish, but an increasing $\bar{N}$ in cisco. Overall, $\bar{N}$ and SI were significantly positively correlated ($r = 0.61$, $t = 2.45$, $P < 0.05$) in Group A whitefish, significantly negatively correlated ($r = -0.73$, $t = 3.35$, $P < 0.01$) in cisco, and not si[illegible]ted ($r = 0.20$, $t = 0.66$, $P > 0.05$) in Group B whitefish.

The seasonal patterns of nine common dominant parasites which affected the diversity of the parasite communities are shown in Figure 9. Details on other parasites are given in Appendices IV to VI.

The seasonal pattern of *D. sagittata* was most obvious in Group A whitefish, in which populations were the greatest. The populations increased from early spring through late summer, then decreased to late fall and fluctuated through the winter. In Group B whitefish, and in cisco, they reached peak populations in the fall and fluctuated irregularly during the rest of the year. The parasites mature in summer and early fall.

In both groups of whitefish, the abundance of *C. truncatus* showed two peaks, in early winter and in midsummer. The abundance of *C. truncatus* in cisco was low and showed no obvious pattern. The cestodes mature in late spring and summer.

The proteocephalids were found primarily in young fish and mainly in summer. The abundance of *P. exiguus* in Group A whitefish increased suddenly to a peak in May, then declined through December, with little or no infection during the winter. The seasonal pattern in Group B whitefish was similar, except that they were present for a much shorter period (May to August) and at much lower abundances. The abundance of *P. filicollis* in cisco peaked in August, with minimum values in winter. Both species appeared to be gravid only in late summer.

In whitefish, *Proteocephalus* plerocercoids were ~~found primarily~~ in the winter, ~~with peak~~ numbers in January. In Group A whitefish, significant numbers were also found in May. In cisco, the abundance peaked in April, then remained at significant levels throughout the summer.

Figure 9. The seasonal patterns in the abundance of nine dominant parasites of Group A (········) and Group B (--------) whitefish, and cisco (——○——)

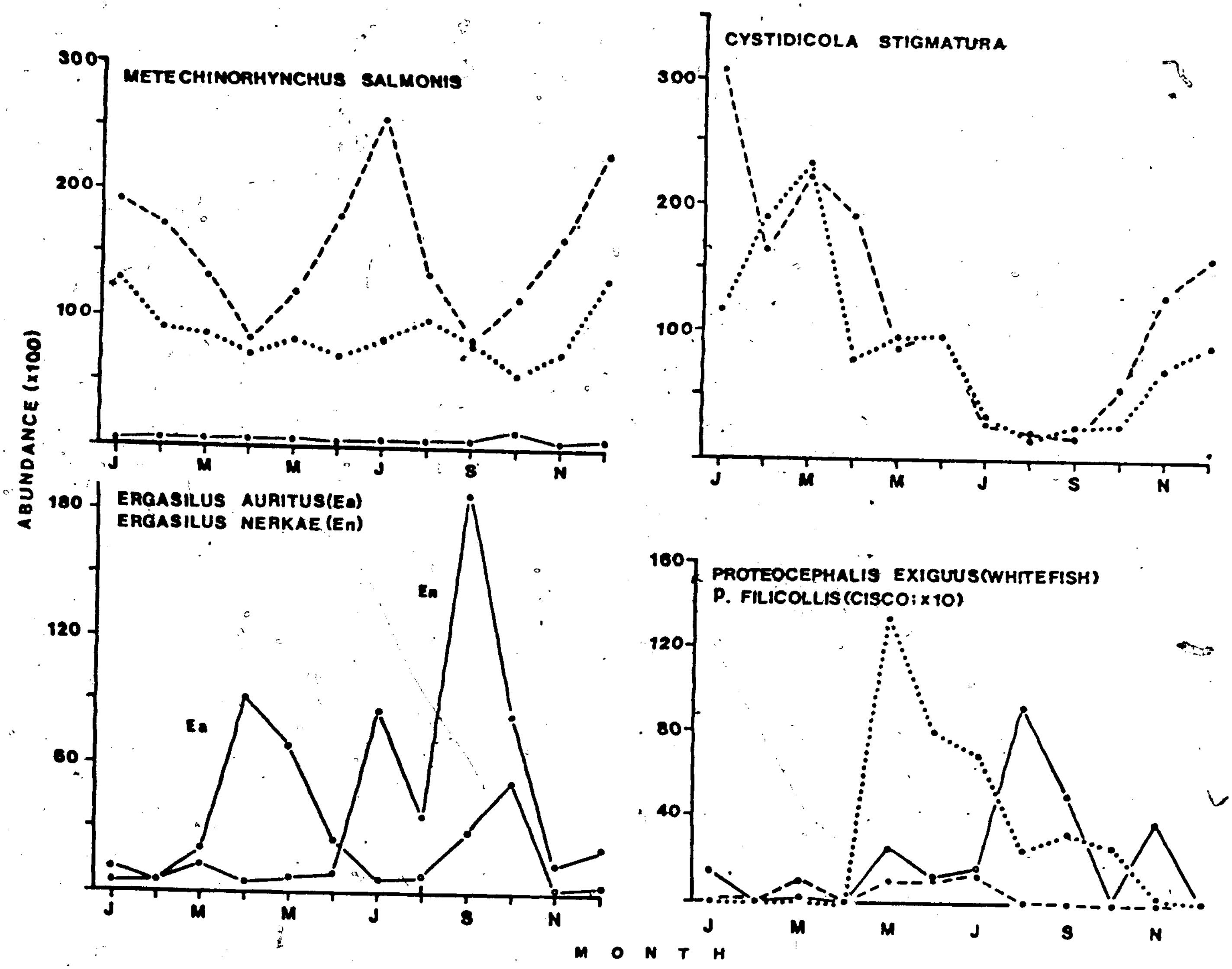
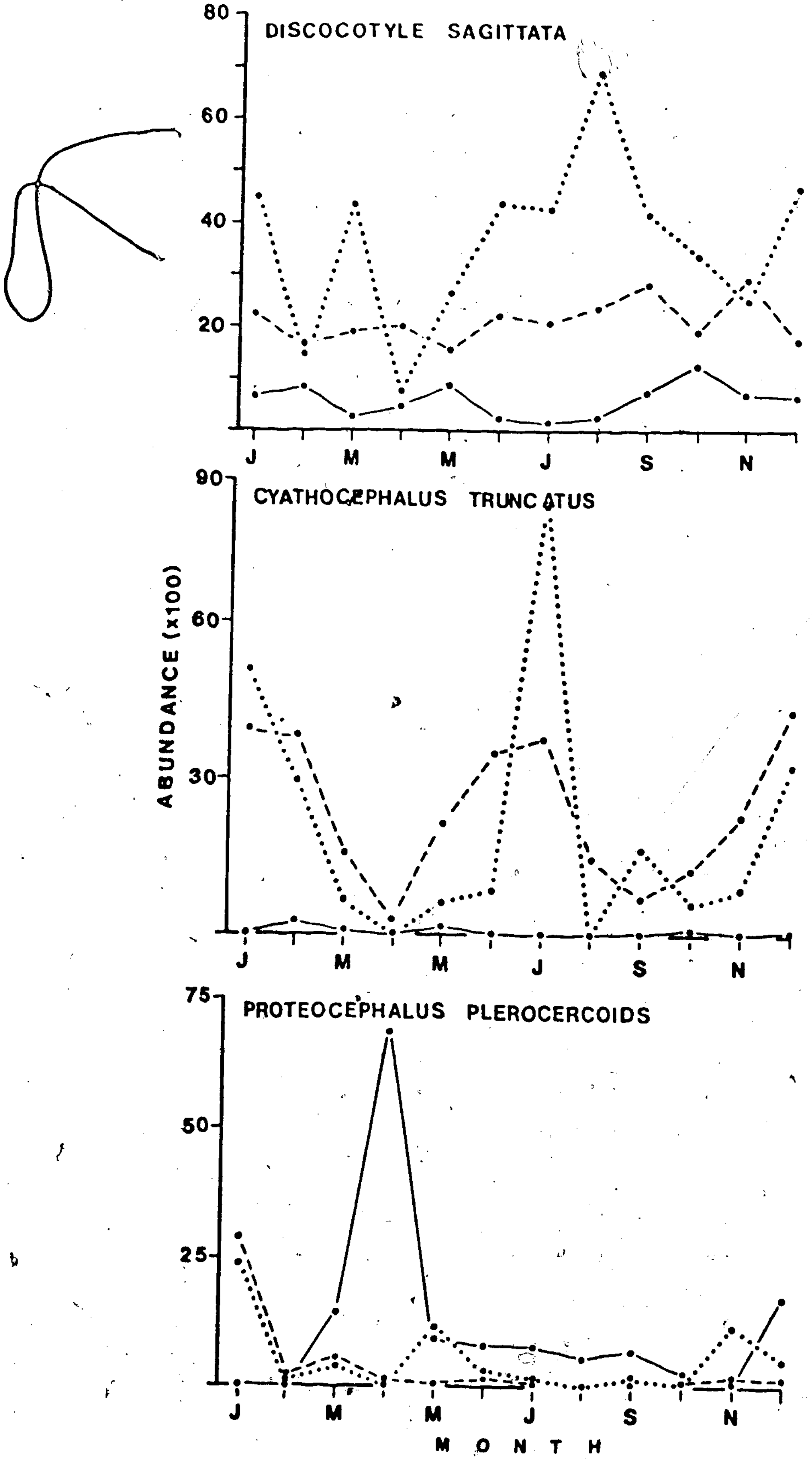

METECHINORHYNCHUS SALMONIS
CYSTIDICOLA STIGMATURA
ERGASILUS AURITUS(Ea)
ERGASILUS NERKAE (En)
Ea
En
PROTEOCEPHALIS EXIGUUS(WHITEFISH)
P. FILICOLLIS(CISCO:x10)
ABUNDANCE (x100)
300
200
100
180
120
60
160
80
40
J
M
M
J
S
N
M O N T H

Figure 9. Continued.


80
DISCOCOTYLE SAGITTATA
60
40
20
J
M
M
J
S
N
90
CYATHOCEPHALUS TRUNCATUS
60
30
ABUNDANCE (x100)
J
M
M
J
S
N
75
PROTEOCEPHALUS PLEROCERCOIDS
50
25
J
M
M
J
S
N
MONTH

Cystidicola stigmatura showed a single, fairly regular cycle of abundance, with maximum values in winter and minimum values in late summer. The parasites mature in spring and summer.

The seasonal pattern of *M. salmonis* was most obvious in Group B whitefish, in which there were peaks in July and December, with minimum values in April and September. In Group A whitefish, the pattern was less obvious, but showed a peak in December. In cisco, the abundance showed very little variation. Gravid female acanthocephalans were found in all three groups of host throughout the year.

The two species of *Ergasilus* were recovered regularly only from cisco, and appeared to show different patterns of abundance. *Ergasilus nerkae* had a single peak in late summer; *E. auritus* had a major peak in April and May, with a smaller peak in September and October. The seasonal abundances of *E. auritus* and *E. nerkae* were negatively correlated ($r = -0.016$, $t = 0.049$, $P > 0.05$); although the correlation was not statistically significant, it did suggest avoidance of direct interaction. In addition, concurrent infections of individual fish with both *E. auritus* and *E. nerkae* were significantly fewer than expected during periods of high populations in June, July and August samples combined ($G = 13.9$, $P < 0.001$) and in December, January and February samples combined ($G = 26.1$, $P < 0.001$). A small proportion of the ergasilids had egg sacs throughout the year; from April to November, a large proportion of each species had egg sacs.

Data on the most abundant parasites in whitefish and cisco were analyzed for differences between years, combining all samples taken between April and September in each of the years 1971 through 1974 (Table 11). (Data from coho are analyzed separately in section VI.)

Table 11. The prevalence and mean intensity (in parentheses) of common parasites recovered in whitefish, cisco and coho in different years

	Group A whitefish		Group B whitefish				Cisco			
	1973	1974	1971	1972	1973	1974	1971	1972	1973	1974
Discocotyle sagittata	76.7 (3.3)	74.0 (4.8)	78.8 (4.9)	71.1 (3.3)	63.5 (2.6)	60.0 (2.2)	38.1 (3.6)	18.8 (2.5)	16.0 (1.8)	13.8 (1.8)
Cyathocephalus truncatus	73.3 (16.7)	64.0 (7.4)	66.7 (30.6)	56.6 (32.0)	79.7 (35.6)	83.3 (31.2)	14.3 (1.0)	1.6 (10.0)	6.0 (2.2)	13.0 (5.4)
Proteocephalus exiguus	60.0 (16.0)	20.0 (26.8)	0	9.2 (8.9)	12.2 (4.9)	13.3 (11.5)				
Proteocephalus filicollis							61.9 (18.9)	26.6 (9.8)	40.0 (13.1)	8.1 (15.8)
Proteocephalus spp.*	13.3 (9.3)	24.0 (20.8)	9.1 (5.7)	5.3 (2.0)	23.0 (16.9)	10.0 (4.7)	81.0 (23.7)	76.6 (58.3)	74.0 (13.5)	11.4 (9.4)
Cystidicola stigmatura	83.3 (6.7)	72.0 (9.0)	39.4 (4.5)	63.2 (7.6)	85.1 (9.6)	70.0 (14.3)	0	7.8 (1.4)	0	0.8 (1.0)
Philonema agubernaculum							4.8 (11.0)	1.6 (5.0)	0	1.6 (5.0)
Metechinorhynchus salmonis	96.7 (98.6)	98.0 (82.6)	100 (220.6)	100 (166.7)	100 (202.6)	100 (193.2)	57.1 (7.8)	26.6 (6.0)	32.0 (5.6)	40.7 (8.0)
Ergasilus nerkae	3.3 (7.0)	4.0 (1.5)	27.3 (5.6)	1.3 (20.0)	0	0	52.4 (64.5)	31.3 (7.3)	41.0 (6.2)	26.0 (4.6)
Ergasilus auritus							33.3 (14.3)	37.5 (29.7)	7.0 (5.0)	14.6 (3.7)
n	30	50	33	76	74	30	21	64	100	123
$\bar{N}$	133.2	118.8	250.4	195.3	247.8	249.2	78.4	66.6	20.8	12.2

*Immature.

Very few consistent, interpretable differences were found. For example, in cisco, $\bar{N}$ showed a continuous, statistically significant ($F = 11.0$, $P < 0.001$) decline from 1971 through 1974. Except for *M. salmonis*, the common parasites in cisco all showed a reduction in prevalence or mean intensity (or both) between 1971 and 1974, but the values in the intermediate years showed almost every conceivable pattern. In addition, $\bar{N}$ in whitefish showed no significant variation between years (F, Group A $= 0.37$; F, Group B $= 1.5$; $P > 0.2$).

During the period of study, there appears to have been an overall decrease in the populations of *D. sagittata* (although this is not shown in data from Group A whitefish), *E. nerkae*, and *E. auritus*; an overall increase in the population of *C. stigmatura*, and no apparent change in the populations of *M. salmonis* and *C. truncatus*. The populations of the *Proteocephalus* spp. appeared to fluctuate irregularly.

Discussion

It was apparent that the patterns of $\bar{N}$ (and the general level of diversity) of the parasite communities in both groups of whitefish were dictated primarily by the abundance of the dominant parasite, *M. salmonis*, but that the patterns of diversity were influenced primarily by numbers of the other common parasites (*C. truncatus*, *Proteocephalus* plerocercoids and *C. stigmatura*). In cisco, where no parasites dominated throughout the season, a higher diversity was the rule, with a particularly high diversity in January, at the same time as in whitefish, and a low diversity only when one parasite became dominant.

In cold temperate lakes, water temperature is traditionally considered to be the major factor determining seasonal patterns in the abundance and activity of both vertebrates and invertebrates. Factors important in determining the abundance and/or maturation of parasites include those of the behaviour of the hosts, particularly their feeding habits, the availability of intermediate hosts, the development of larval parasites in those intermediate hosts, and the resistance of fish to infection. Since changes in temperature may have different effects on each of these factors, the seasonal patterns of abundance and/or maturation of parasites may be complex, and may differ between parasites or between hosts.

The most important aspect of host behaviour is the feeding behaviour, which is considered to be of sufficient importance to deserve a separate section (V, C). Another aspect of behaviour important in determining the seasonal patterns in the parasite community is the migration of whitefish into deeper water as the lake warms up in late summer. At this time, the intensities of *C. truncatus* and *M. salmonis* decrease. Trout undergo similar migration; the effect on the parasites is presumably the same.

I did not study the availability of intermediate hosts, except as availability was reflected in the stomach contents of the fish. However, Larkin (1948) showed that the young of *P. affinis*, intermediate host for both *C. truncatus* and *M. salmonis*, were born in winter and could survive for more than two years. In this case, at least, availability of the intermediate host does not seem to be a major factor in producing the observed seasonal patterns.

Larval *C. stigmatura* were found in whitefish throughout the year, suggesting that infected intermediate hosts, *Gammarus lacustris*, were also available throughout the year. The total abundance of *C. stigmatura* reached maximum values in winter, as did that of the other parasites in this study. However, the maximum numbers of adult specimens were found in spring and early summer. These observations suggest a basic annual cycle for *C. stigmatura*, with the adults reproducing in spring and summer, larvae developing in the amphipod intermediate host during the warm water period of the summer, and reinfection of the whitefish in the fall.

The proteocephalids seem to show a similar cycle with maturation in the early summer; however, reinfection of the definitive hosts did not seem to take place until late winter or early spring, as indicated by the sudden influx of immature *Proteocephalus* (plerocercoids). Most of the *Proteocephalus* plerocercoids encountered in whitefish were probably immature *P. exiguus*, and most of those in cisco were probably immature *P. filicollis*, as indicated by the peak in each of these species shortly after the peak in plerocercoids. This maturation in summer appears to be a general rule among proteocephalids, and has been reported for *P. stizostethi* (Connor, 1953), *P. ambloplitis* (Fisher and Freeman, 1969), *P. filicollis* (Hopkins, 1959; Chappell, 1969a) and *P. pearsei* (Tedla and Fernando, 1969; Cannon, 1973). However, most of these other species have immatures (plerocercoids) present through the year, sometimes (as in *P. ambloplitis*) in the tissues. Such immatures were not found in this study, suggesting that copepods with infective plerocercoids were available to the fish until late winter or early spring.

Several parasites, such as *C. truncatus*, *C. stigmatura* and *M. salmonis* in whitefish, and *D. sagittata* in cisco, showed peak abundances in the winter, during the period of coldest temperatures. The pattern may be due to a reduction in resistance of the fish at low temperatures.

Kennedy (1970, 1972) has shown experimentally that initial establishment of *Caryophyllaeus laticeps* in *Leucicus idus* and *Pomphorhynchus laevis* in *Carassius auratus* is higher at low temperatures than at high temperatures. After the initial establishment, higher temperatures had little effect. Similarly, Awachie (1972) found that more *Echinorhynchus truttae* became established in *S. trutta* at low temperatures than at high temperatures.

The only case of apparent seasonal segregation of two species involved the two species of *Ergasilus*. This may be an adaptive strategy maximizing the use of the limited available space on the gill filaments of the stunted cisco. *E. nerkae* produced only a single generation a year, with maximum populations and reproduction in late summer. *E. auritus*, on the other hand, appeared to produce two generations per year; the major period of reproduction occurred in late spring, when populations of *E. nerkae* were at a minimum. The second period of reproduction was in early fall, partly overlapping that of *E. nerkae*; however, at this time, the two species were essentially on different fish, as indicated by the number of concurrent infections, which were significantly less than expected by chance.

C. FOOD HABITS

The significant effects of age of the host and seasons on the parasite communities may be due to changes in the food habits of the hosts. Therefore, the food habits of the common, large fishes (whitefish, cisco, trout, coho, pike and burbot) were examined.

The prevalence of food items in the diet of these fishes is shown in Table 12. Each species fed primarily on a few specific food items

Table 12. The prevalence, indices of dominance and indices of diversity of food in various fish in Cold Lake, Alberta

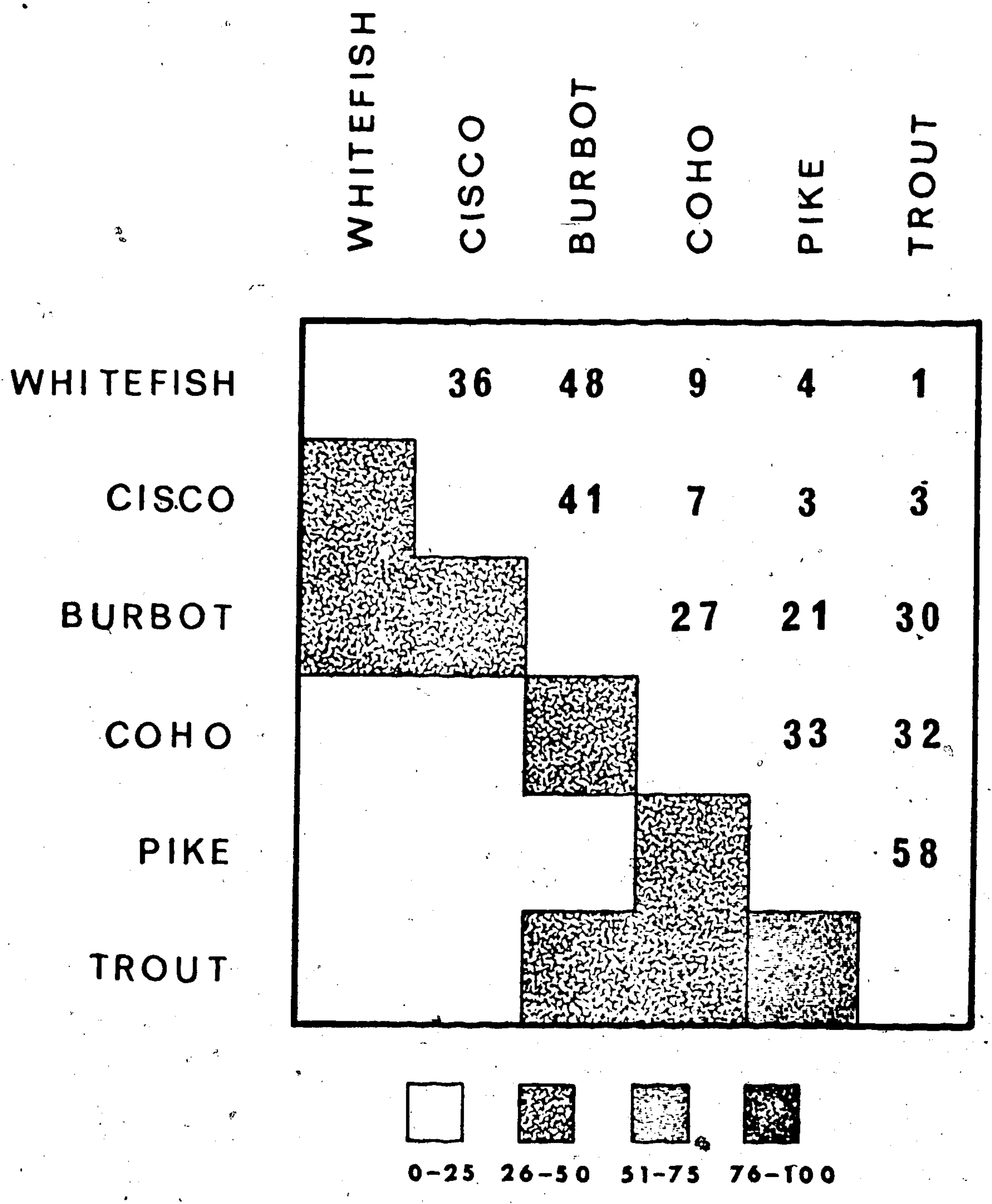
		Whitefish	Cisco	Trout	Coho	Pike	Burbot	Dominance Indices
Food Items								
Whitefish					4.8	3.6		0.013
Cisco				25	9.1	3.6	33.3	0.14
Cyprinid					1.6	14.3		0.046
Walleye					0.5			0.0001
Sticklebacks		1.6	4.1	75	34.9	64.3	33.3	2.8
Burbot						3.6		0.012
Sculpin						28.9	6.7	0.11
Fish Eggs		10.9	5.5				6.7	4.61
TOTAL FISH		12.5	9.6	100	50.9	118.3	80	7.73
Copepoda			40.4					21.54
Mysis relicta		19.9	21.2		0.5		13.3	14.38
Pontoporeia affinis		75.5	6.8		1.6		40.0	15.23
Hyallela azteca		12.0	7.5				20.0	5.89
Gammarus lacustris		19.9	17.2		0.5		53.3	12.37
TOTAL AMPHIPODS		107.4	31.5		2.1		113.3	33.49
TOTAL CRUSTACEANS		127.3	93.1		2.6		126.6	69.41
Ephemeroptera		2.5	11.0		1.1			6.25
Odonata			0.7		4.3			0.37
Hemiptera		0.5			13.4			0.079
Trichoptera		12.8			51.6		6.7	1.98
Coleoptera					6.5			0.0014
Diptera		54.5	0.7		7.0			0.67
TOTAL INSECTS		70.3	12.4		83.9		6.7	9.35
Sphaeriidae		63.8	2.1				6.7	10.84
Planorbidae		0.3						0.046
Physidae		4.6						0.70
TOTAL MOLLUSKS		68.7	2.1				6.7	11.59
Nematomorpha		0.5	0.7					0.45
Glossiphonidae		11.4			0.5	3.6		1.74
No. Examined	(n)	497	323	30	288	61	19	
No. with Food		367	146	20	186	28	15	
No. Food Items	(F)	15	12	2	15	7	10	
Mean No. Food Items (± S. E.)	($\bar{F}$)	2.69 (±0.06)	1.25 (±0.04)	1.0	1.5 (±0.06)	1.25 (±0.1)	2.6 (±0.27)	
Simpson's Index	(SI(F))	5.0	4.44	1.60	5.24	2.84	6.53	
Shannon-Weaver Index	(H'(F))	1.93	1.87	0.56	1.94	1.35	2.04	
Evenness	(E(F))	0.69	0.60	0.79	0.72	0.64	0.87	

with others taken in smaller proportions. Whitefish fed primarily on *Pontoporeia affinis*, Diptera (mainly Tendipedidae) and Sphaeriidae; cisco on copepods, *Mysis relicta* and *Gammarus lacustris*; trout and pike fed mainly on fish, particularly sticklebacks; coho on Trichoptera and sticklebacks; and burbot on *G. lacustris*, *P. affinis*, cisco and sticklebacks.

Whitefish, cisco, coho and burbot all had relatively diverse diets, as indicated by the number of types of food consumed (F) and by the diversity indices SI(F), H'(F) and E(F) (see Table 12 for abbreviations). In whitefish and burbot this diversity was due to a diverse diet in individual fish, as indicated by high values for the mean number of food items ($\bar{F}$); in cisco and coho, the lower $\bar{F}$ values suggest that individual fish tend to have more restricted diets (at least at any one time). Pike and especially trout had diets with low diversity (low F, $\bar{F}$, SI(F), and H'(F) values), although the small number of items eaten were consumed in fairly even proportions (high E(F) values). There was no correlation between food diversity (Table 12) and parasite diversity (Table 4).

As might be expected, there was a relatively low degree of similarity in diet among these fishes (Figure 10). Two overlapping clusters were apparent, with whitefish, cisco and burbot forming one cluster, and trout, coho, pike and burbot forming another. The first cluster appears to be due to the high prevalences of *Mysis relicta* and amphipods in the diets of all three fishes. The second, and particularly the high similarity between trout and pike, appears to be due to the high prevalence of sticklebacks in the diets of those fishes. There was no correlation between similarity in diet and similarity in parasites.

Figure 10. Trellis diagram showing percent similarity of diets in large fishes in Cold Lake, Alberta



	WHITEFISH	CISCO	BURBOT	COHO	PIKE	TROUT
WHITEFISH		36	48	9	4	1
CISCO			41	7	3	3
BURBOT				27	21	30
COHO					33	32
PIKE						58
TROUT						

One reason for the lack of correlation between diet and parasites is that dietary items differ in the number and kinds of parasites they carry to fishes (Table 13). (*Metechinorhynchus salmonis*, which are carried by both amphipods and fishes, have been allocated to these two types of dietary items according to the relative flow rates shown in Figure 23.) The greatest numbers of species of parasites are acquired by ingestion of copepods, direct attack by free-living larvae, and by ingestion of fish. In contrast, the greatest proportion of individuals (sum of dominance values) are acquired by ingestion of amphipods.

Diets may change with age of the hosts; therefore, the food habits of whitefish age classes II to IX were examined. The percentage of the fish containing food varied, but without apparent relationship with age. F and $\bar{F}$ increased gradually with age (Figure 11). Diversity, as indicated by SI(F) gradually increased to age class VI, then decreased (Figure 11). The decrease appeared to be due largely to an increase in prevalence of *P. affinis* in the diets of the older fish (Appendix VII). The diversity of food items (SI(F)) was not correlated with the diversity of parasites (SI) in fish of the same age ($r = -0.62$, $t = 1.94$, $P > 0.10$).

Because of the significant effects of age on diets, and in order to try to correlate any patterns in diet with those in the parasites, the effects of seasonal changes in diets were examined within the same groups used for analyzing the effects of seasonal changes on parasite communities.

Few Group A whitefish (age classes IV and V) collected in March and April contained food, although most collected from May through September, and almost all collected from October through February, contained food (Figure 12). Sample sizes are small (Appendix VIII), but $\bar{F}$ appears to be

Table 13. The number of items in the diet, number of parasite species and the sum of dominance indices of food items and of parasite species from various sources by the community of fish

Sources of parasites	Food items		Parasite species	
	No.	Sum of dominance indices	No.	Sum of dominance indices
Active free-living stage	-	-	9	17.42
By ingestion:				
Copepods	1	21.54	10	19.57
Amphipods	3	33.49	4	60.58
Fish	8	7.73	8	2.39
Molluscs	3	11.59	4	0.16
Others	9	26.12	5	0.17

Figure 11. The diversity (No. food items (F) (-·-·-·-), mean no. food items ($\bar{F}$) (————), and Simpson's Index (SI(F)) (-------)) of food in various ages of whitefish. Vertical bars for $\bar{F}$ indicate ± standard error.

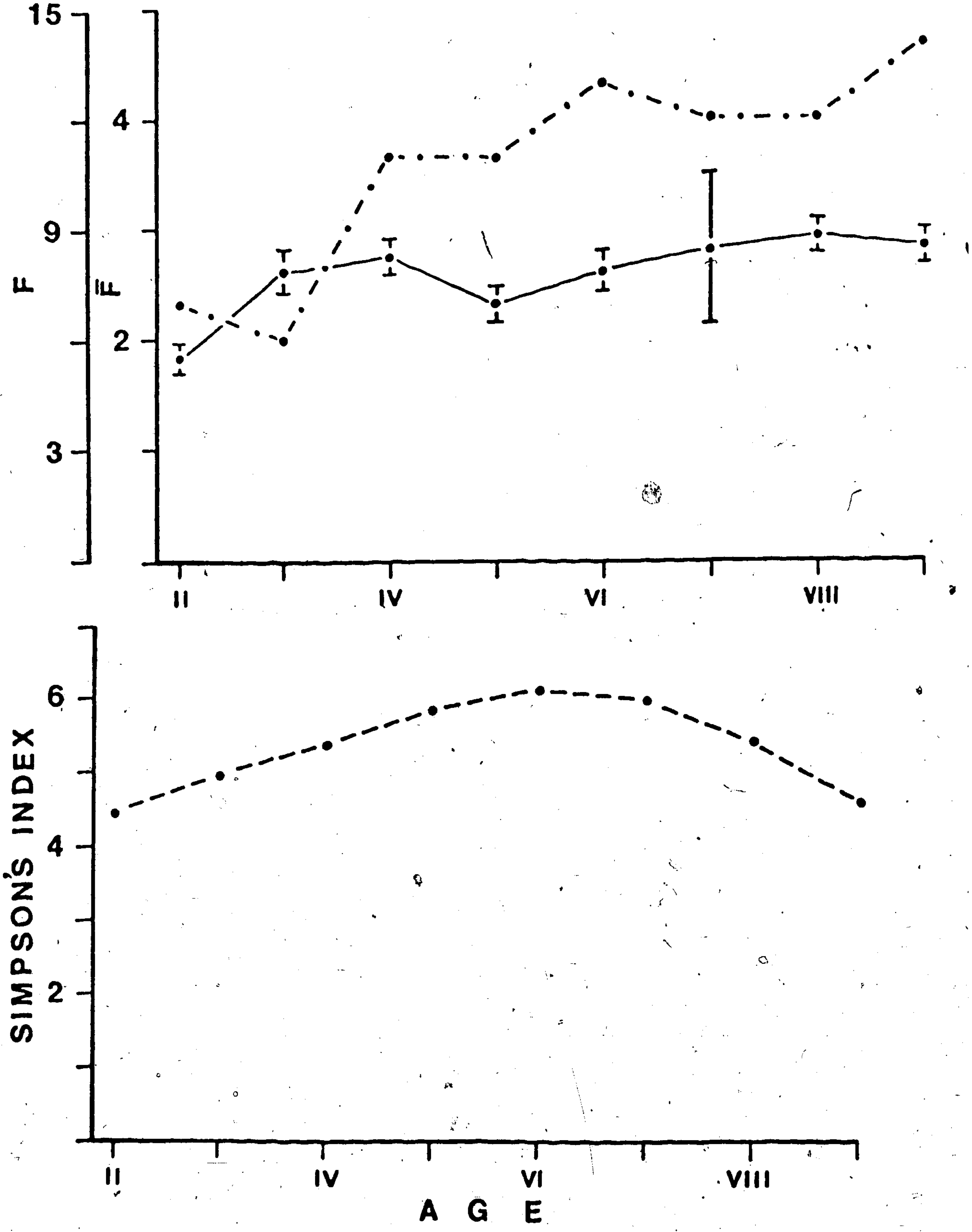
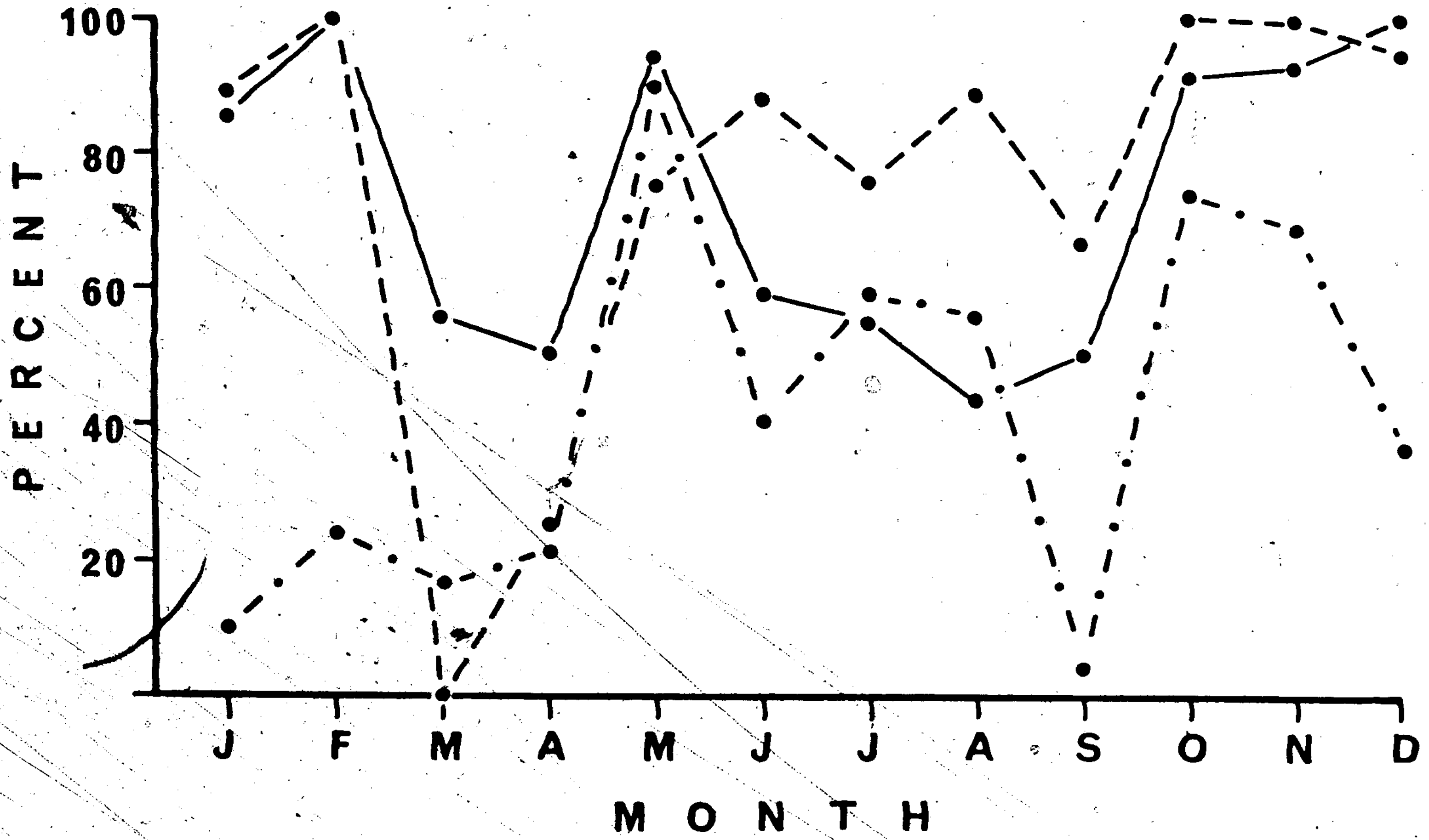

15
4
9
2
3
F
F̄
II
IV
VI
VIII
6
4
2
SIMPSON'S INDEX
II
IV
VI
VIII
A G E

Figure 12. Percent with food in stomach of Group A (--------) and Group B (————) whitefish and of cisco (-·-·-·-)

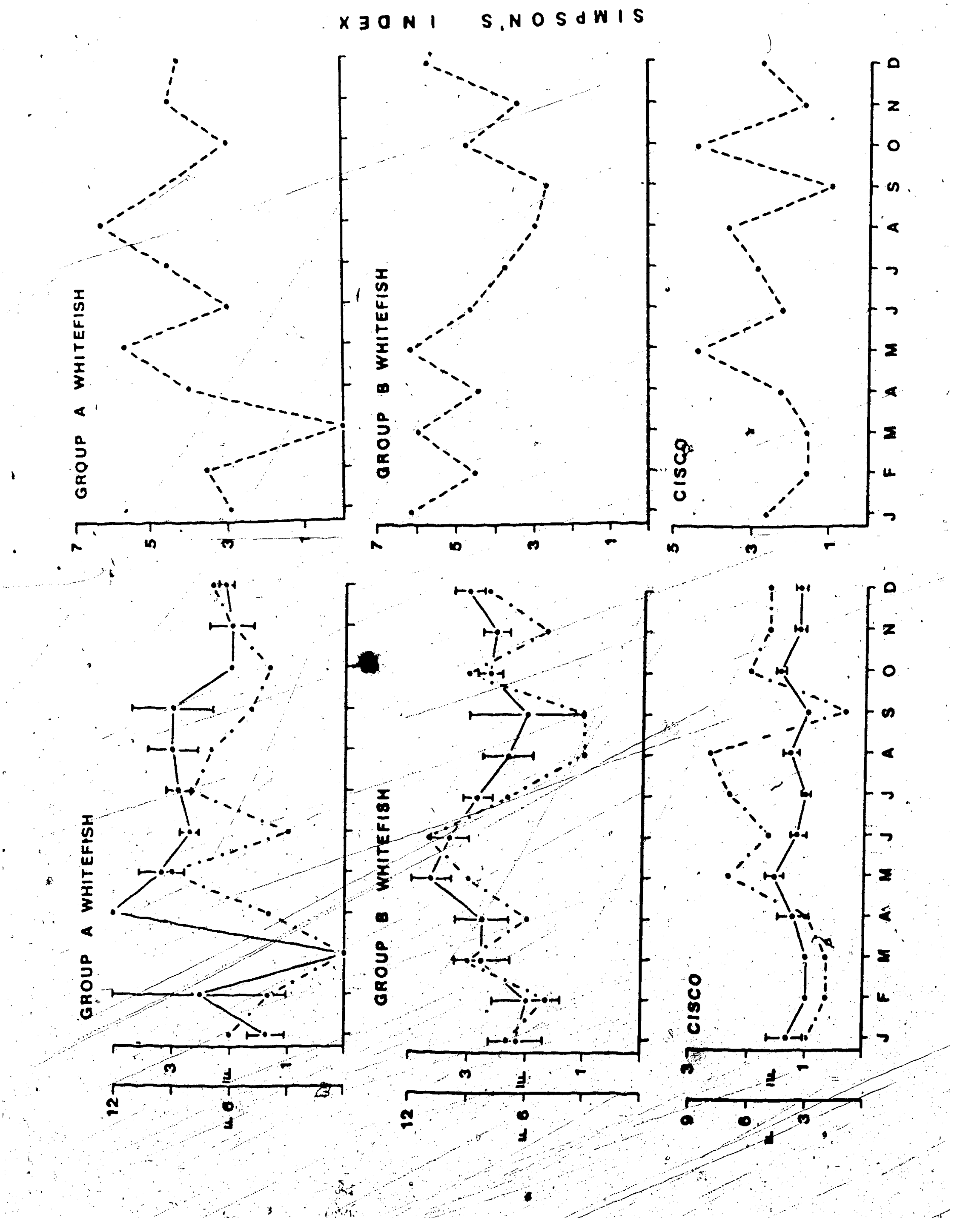

PERCENT
100
80
60
40
20
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

higher from May through September (overall mean, 2.9) than from October through February (overall mean, 1.9) (Figure 13). SI(F) varies considerably (Figure 13); from May through September, though, the food is consistently dominated by *P. affinis*, tendipedids, and sphaeriids (Appendix VIII), with an overall SI(F) of 4.69; from October through February, *Mysis relicta*, *G. lacustris* and fish eggs join the dominants at various times, the overall SI(F) being 6.07.

Most of the Group B whitefish (age classes VII and VIII) taken in May or from October through February contained food; only about half of those taken at other times contained food (Figure 13). Again, sample sizes are small (Appendix IX); both $\bar{F}$ and SI(F) had high values in May, declined through September, then increased through December (Figure 13). The prevalence of *P. affinis* was high throughout the year (except in March), tendipedids were prevalent primarily in the summer, and sphaeriids in summer and fall; other amphipods, trichopterans, and fish eggs were dominant items at various times, mostly during the winter (Appendix IX).

Almost all of the cisco (age classes IV and V) had food in their stomachs during May, about half contained food from June through August, virtually none in September, most in October and November, and relatively few in December through April (Figure 13). Individual fish contained very few food items ($\bar{F}$ was low and showed little seasonal variation), but the population had a more diverse diet (F, SI(F)) in the summer (especially in May and August) and in October (Figure 13). The dominant items in the diet varied, with *M. relicta* more prevalent in the win[illegible] mayflies and amphipods in May, and copepods at various times, esp[illegible] in the summer and fall (Appendix X). The high prevalence of copepods in

Figure 13. Seasonal diversity (No. food items (F) (-·-·-·-), mean no. food items ($\bar{F}$) (————), and Simpson's Index (SI(F)) (--------)) of food in whitefish and cisco


SIMPSON'S INDEX
GROUP A WHITEFISH
GROUP B WHITEFISH
CISCO
GROUP A WHITEFISH
GROUP B WHITEFISH
CISCO
F
F
12
6
3
1
9
6
3
7
5
3
1
J F M A M J J A S O N D

the few cisco containing food in March is noteworthy, as is the low prevalence of *P. affinis* throughout the year.

Ninespine sticklebacks were an important food source for the predatory fishes in Cold Lake. Most of the parasites of sticklebacks (9 of 13 species) are in a larval stage; five of them mature in the predatory fishes. These facts suggest that sticklebacks are important intermediate and/or transport hosts within the Cold Lake ecosystem. Therefore, the parasite fauna, particularly the larval forms, of ninespine sticklebacks was investigated with particular reference to parasite transmission within the ecosystem.

Samples of sticklebacks collected by seining in water ½ to 1 m deep, by minnow trap set in water 3-4 m deep, or taken from the stomachs of trout or pike differed significantly in sex ratio and size distribution (Figure 14). Seined sticklebacks were smaller than those collected by other means, with a slight preponderance of females. Trapped sticklebacks were larger, with a marked preponderance of males. Sticklebacks from the stomachs of predatory fish were also large, but with a marked preponderance of females.

The parasite faunas of sticklebacks collected by various methods differed markedly (Table 14). Males, regardless of how collected, were more frequently infected than females with the trematode *Bunodera luciopercae*, and those collected by seining were less frequently infected with *E. auritus*, *T. nodulosus* and *M. salmonis*. These differences were partly, but not completely, due to the larger sizes of the females (Figures 15-16).

Sticklebacks seined in shallow water had a larger proportion infected with *S. solidus* than did those trapped in deeper water. The

Figure 14. The percent distribution of different sizes sticklebacks collected by seining (S), trapping (M), and recovered from stomachs of trout (T) and of pike (P)

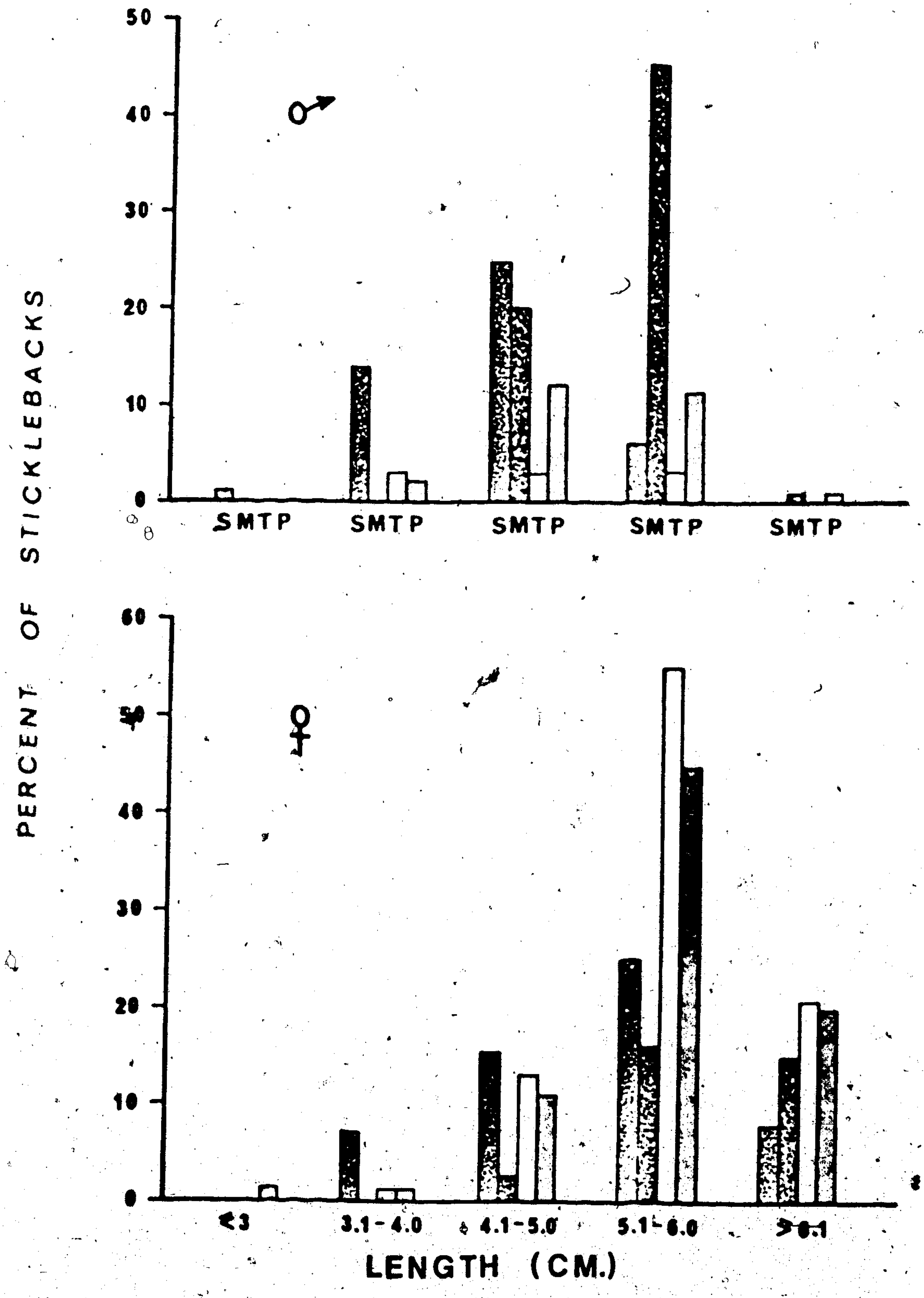

PERCENT OF STICKLEBACKS
50
40
30
20
10
0
♂
SMTP
SMTP
SMTP
SMTP
SMTP
60
50
40
30
20
10
0
♀
<3
3.1-4.0
4.1-5.0
5.1-6.0
>6.1
LENGTH (CM.)

Table 14. The prevalence of parasites of ninespine sticklebacks collected by seining, trapping, recovered from stomachs of trout and pike. Summarized diversity values at the bottom table are based only on nine species recovered from sticklebacks from fish stomachs.

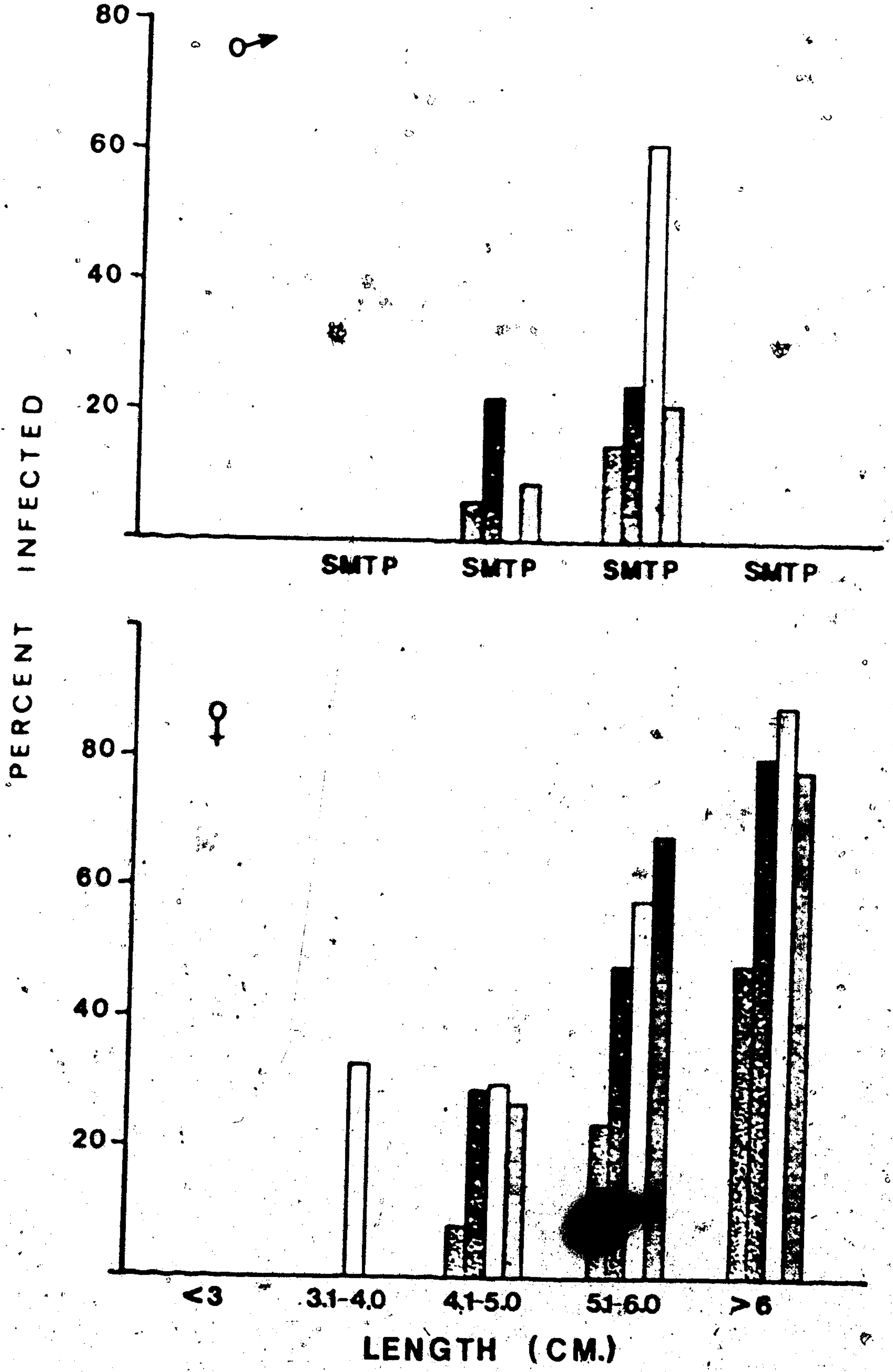
	Seined			Trapped			In trout			In pike		
	M*	F	Total	M	F	Total	M	F	Total	M	F	Total
Gyrodactylus sp.	48.6	47.7	48.1	77.0	86.3	80.2	NOT EXAMINED					
*Apatemon gracilis***	12.7	16.0	12.4	9.2	7.5	8.6	NOT EXAMINED					
*Cotylurus erraticus***	48.1	42.3	44.8	47.4	46.3	47.0	NOT EXAMINED					
*Diplostomum spathaceum***	63.5	70.3	67.4	88.2	87.5	87.9	NOT EXAMINED					
Bunodera luciopercae	5.1	2.7	3.7	7.9	3.8	6.5	0	0	0	2.1	0.6	1.0
Eubothrium spp.***	4.8	4.2	4.5	3.9	5.0	4.3	0	0	0	6.4	1.9	3.0
Proteocephalus filicollis	11.3	12.9	12.1	8.6	12.6	9.9	0	2.2	2.0	4.3	5.8	5.3
*Schistocephalus solidus***	56.3	27.1	40.0	2.0	3.8	2.6	0	0	0	2.1	0	0.5
*Triaenophorus nodulosus****	7.3	16.0	12.1	9.2	16.3	11.6	5.3	16.3	15.3	14.9	16.0	15.8
Raphidascaris sp.***	0	0.4	0.2	0	0	0	0	0.5	0.3	0	0	0
*Metechinorhynchus salmonis****	5.9	20.6	14.1	2.3	60	35.8	21.1	58.2	54.7	21.3	64.1	54.2
*Pomphorhynchus bulbocolli****	0.6	0.2	0.4	1.3	1.3	1.3	0	1.1	1.0	0	0.6	0.5
Ergasilus auritus	2.8	13.1	10.0	11.2	48.8	24.1	10.5	29.9	28.1	12.8	22.4	20.2
No. examined		806			232			203			203	
No. spp.		9			8			6			8	
Mean no. spp. (±S.E.)		2.22 (±0.05)			3.19 (±0.09)			1.59 (±0.06)			1.88 (±0.11)	
Mean no. ind. per inf. fish (±S.E.)		3.94 (±0.23)			6.57 (±0.38)			3.26 (±0.21)			3.51 (±0.25)	
Simpson's index		5.59			3.69			2.09			2.0	
Shannon-Weaver index		1.84			1.57			0.98			1.01	
Evenness		0.81			0.72			0.54			0.49	

* M - Male, F - Female

** Larval forms maturing in piscivorous birds

*** Larval forms maturing in fish

Figure 15. The prevalence of *Metechinorhynchus salmonis* in sticklebacks of different sizes collected by seining (S), trapping (M), or recovered from stomachs of trout (T) and of pike (P)



80
60
40
20
♂
SMTP
SMTP
SMTP
SMTP
PERCENT INFECTED
80
60
40
20
♀
<3
3.1-4.0
4.1-5.0
5.1-6.0
>6
LENGTH (CM.)

Figure 16. The prevalence of *Triaenophorus nodulosus* in sticklebacks of different sizes collected by seining (S), trapping (M), or recovered from stomachs of trout (T) and of pike (P)

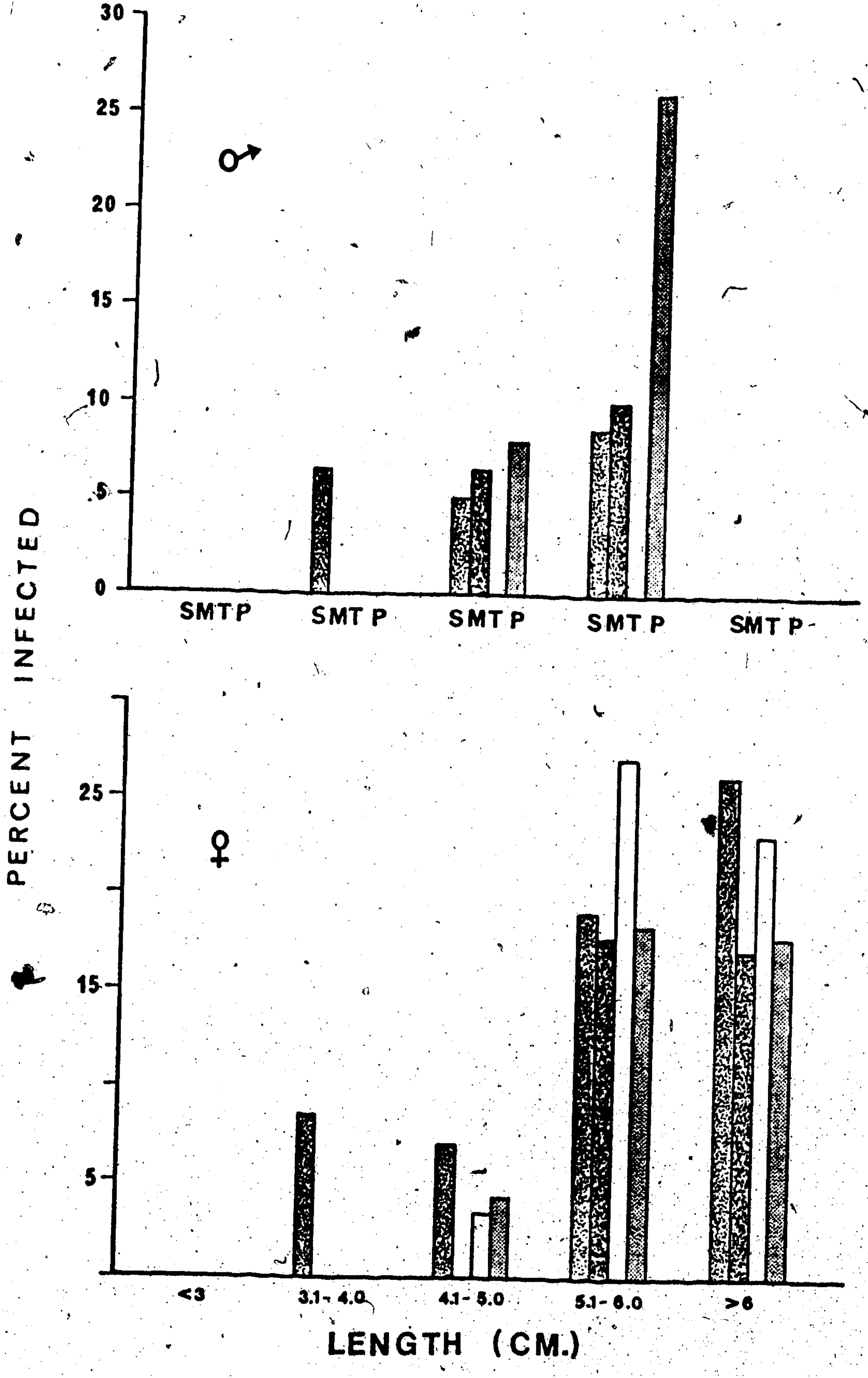
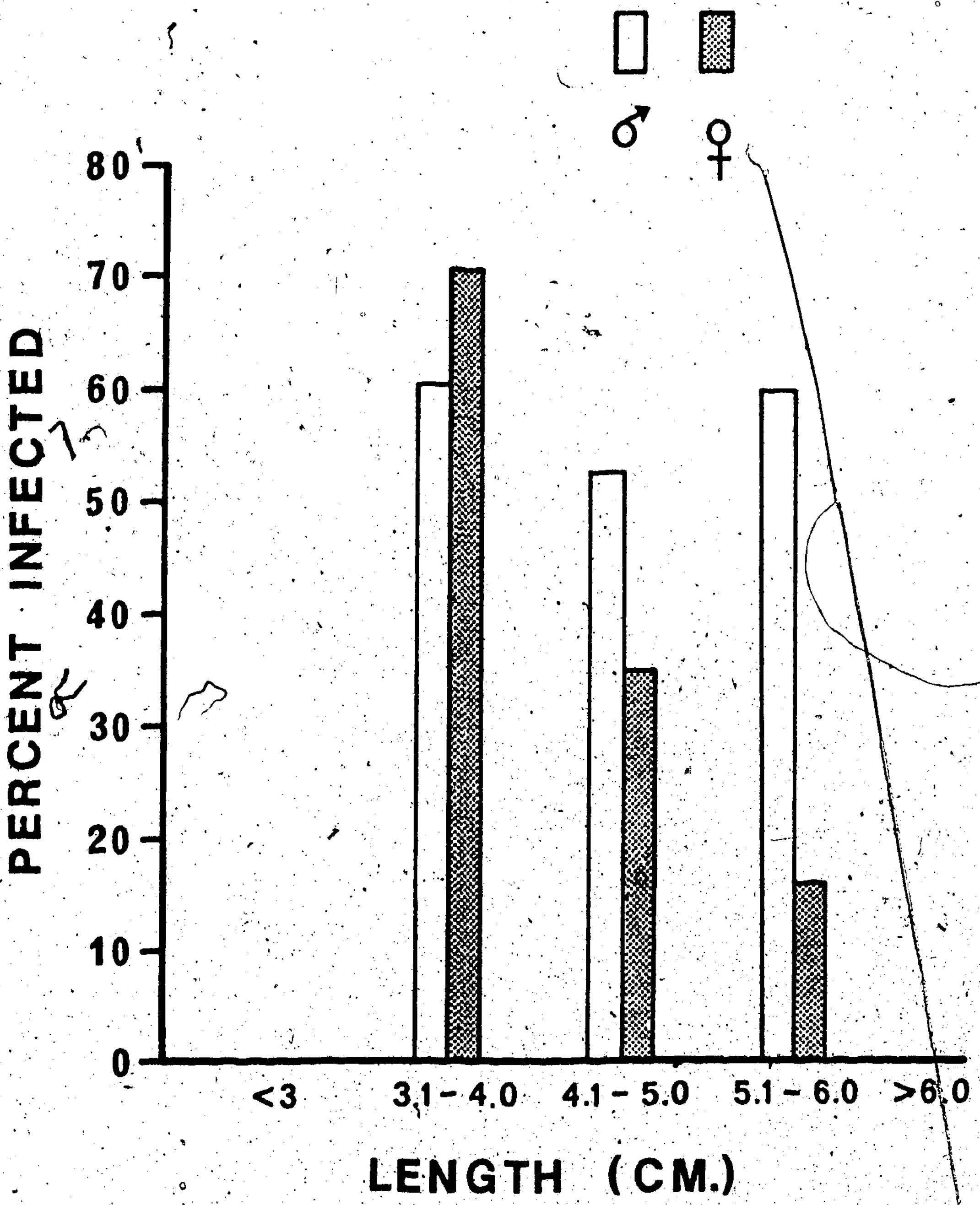

30
25
20
15
10
5
0
♂
SMT P
SMT P
SMT P
SMT P
SMT P
PERCENT INFECTED
25
15
5
♀
<3
3.1- 4.0
4.1- 5.0
5.1- 6.0
>6
LENGTH (CM.)

Figure 17. The prevalence of *Schistocephalus solidus* in sticklebacks of different sizes collected by seining


♂
♀
PERCENT INFECTED
80
70
60
50
40
30
20
10
0
<3
3.1 - 4.0
4.1 - 5.0
5.1 - 6.0
>6.0
LENGTH (CM.)

trapped sticklebacks had a larger proportion infected with *Gyrodactylus* sp., *D. spathaceum*, *M. salmonis* and *E. auritus* than did shallow-water sticklebacks. These differences are partly, but not entirely, due to the larger fish in the sample of trapped sticklebacks (Figure 14). In part, they also may be due to behavioural changes in sticklebacks infected with *S. solidus*, which move into shallower, warmer waters (Lester, 1971). The presence of *S. solidus* was significantly negatively correlated with that of *D. spathaceum* and *M. salmonis* (and with that of *C. erraticus* and *T. nodulosus* as well) (Table 15).

Sticklebacks taken from the stomachs of trout or pike were frequently partly digested, making it difficult to tell whether the ectoparasitic monogenean, *Gyrodactylus* sp., or the metacercariae of *A. gracilis*, *C. erraticus* or *D. spathaceum* were present or not. Therefore, these four species have not been included in the following analyses.

Sticklebacks eaten by predatory fishes resembled those taken by minnow trap in size (Figure 14), and in having a low prevalence of *S. solidus* but high prevalences of *E. auritus* and *M. salmonis* (Table 14). They had higher mean numbers of individuals per fish, but lower indices of diversity, than trapped (or seined) sticklebacks (Table 14).

Discussion

Each species of fish examined showed a distinct preference for specific, generally different food items. As a result, each species has a specific food niche within the ecosystem.

Whitefish feed in the benthic zone, mostly on *P. affinis*, tendipedids, and sphaeriids. These three items also made up the majority of their food in other studies in lakes where cisco were present (Koelz,

Table 15. Concurrent infections between *Schistocephalus solidus* and other larval parasites in ninespine sticklebacks collected by seining.

	Schistocephalus solidus		
Number of fish infected with:	Present (322)	Absent (48[illegible])	Significance*
Cotylurus erraticus	128	226	HS (neg)
Diplostomum spathaceum	164	379	HS (neg)
Triaenophorus nodulosus	17	77	HS (neg)
Metechinorhynchus salmonis	22	112	HS (neg)
Apatemon gracilis	41	60	NS
Eubothrium spp.	31	36	NS
Raphidascaris sp.	0	2	NS

*HS - highly significant ($P < 0.001$) (G-statistics, Sokal and Rohlf, 1969). NS - not significant.

1929; Hart, 1931; Rawson, 1959, 1960; Koshinsky, 1965; Rechahn, 1970); in lakes where cisco were not present they also fed extensively on plankton (Bidgood, 1973). The general conclusion has been that their food habits depend on the availability of different items within the food niche they can occupy.

Cisco feed primarily on plankton, or on organisms that periodically enter the plankton, such as *Mysis*, amphipods, or aquatic insects (Pritchard, 1931; Dryer and Beil, 1964). They normally feed in the epilimnetic zone.

Lake trout are limited to cold water; in the summer, they occupy the hypolimnion, where they feed mainly on fish, mostly cisco. In the spring, with cooler water, they feed mainly on sticklebacks which begin to congregate, soon after ice break-up, in the shallow water (Roberts, 1975). In most studies, cisco appear to be the preferred prey (Rawson, 1959, 1961; MacCrimmon and Skobe, 1970; Martin, 1970) but in Lake Ontario alewives (Dymond, 1928) and in Lake Superior smelt (Dryer *et al.*, 1965) were of primary importance, suggesting that availability is a major factor.

Pike are predators which occupy primarily the littoral zone, feeding almost exclusively on fish of whatever species are available (Lawler, 1965). In Cold Lake, they feed largely on sticklebacks, competing with trout in the spring, but not in the summer.

The types of food consumed by burbot depend on their size; those over 50 cm feed exclusively on fish, of whatever species of fish are available (Van Oosten and Deason, 1938; Clemens, 1951; Wagner, 1972), and those under 50 cm feed mainly on invertebrates (Clemens, 1951). Most of the burbot in my studies were less than 50 cm and had fed mainly on invertebrates. They shared the benthic zone with whitefish and compete with them for *P. affinis* and, to a lesser extent, other amphipods.

Thus each of the larger native fishes has a special food niche, overlapping others only slightly. Young introduced coho also appear to have a separate food niche. In Cold Lake, as in Lake Michigan (Peck, 1974), or various lakes in Colorado (Klein and Fennell, 1969) or Wisconsin (Avery, 1973; McKnight and Serns, 1974), young coho fed mainly on insects. However, older coho usually, but not always, switch to a diet composed primarily of fish. In the ocean, fish comprise about 80 percent of their diet (Prakash, 1962); in the Great Lakes, the larger coho feed principally on smelt and alewives (Scott and Crossman, 1973). In Cold Lake, too, the larger coho (age class III) fed primarily on fish: 82 percent of those with food in the stomach had fed on fish, primarily sticklebacks and cisco. The food niche of the larger coho in Cold Lake, therefore, had a considerable overlap with those trout and pike. The limited food niche for older coho in Cold Lake may have contributed to the failure of this introduction.

In temperate lakes, temperature has a profound influence on the diet, rate of feeding and rate of digestion of the fish. Data, such as I have presented, on the proportion of stomachs containing food depend upon both the rate of feeding and the rate of digestion. There appears to be no information in the literature on the effect of temperature on these rates in the species of fishes I have examined, but Brett and Higgs (1970) have examined the effects of temperature on these rates in another cold-water fish, fingerling sockeye salmon. The situation appears to be complicated by temperature compensation in both feeding and digestion rates, but primarily the former, at low temperatures. However, their data would suggest that maximum meal size is reduced at low temperature, and that the average meal would take about 33 days to digest at 1 C, about 6 days at 3 C, but less than 1 day at 15 C or above.

Although some whitefish and cisco have food in their stomachs throughout the year, incorporation of the rates of digestion indicated by Brett and Higgs' work suggests that the rate of feeding is relatively low during the period of ice cover, that there is a tremendous increase in feeding after ice break-up when temperatures are rising, and that the fish are actively feeding throughout the summer, despite the high proportion of emptied stomachs. There appears to be evidence of reduced feeding prior to spawning, then increased feeding after spawning. These presumed feeding rates appear to correlate nicely with the observed numbers of *M. salmonis*, at least in whitefish.

The absence of any correlation between the diversity of foods and the diversity of parasites is not surprising; it appears to be due to a combination of three factors. First, the individual food items vary greatly in importance as intermediate or transport hosts for parasites. Amphipods are obviously very important, as are copepods and, to a lesser extent, fish. Molluscs, insects and mysids appear to be relatively unimportant.

Second, some food items that must have been eaten on the basis of the parasites recovered, were not found in the food habit studies. For example, no copepods were found in whitefish, but the significant numbers of proteocephalids indicate that copepods must have been eaten. Using similar arguments, Collins and Dechtiar (1974) deduced from the parasite fauna recovered from introduced kokanee salmon in Lake Huron the kind of food items which might have been consumed by the salmon.

Third, even if several species of fishes ingest the same kinds of larval stages, host specificity can affect the kinds of parasites which will develop. *Gammarus lacustris*, the intermediate host of *C. stigmatura*, were eaten in substantial numbers by whitefish, cisco, coho and burbot; the first three harboured the nematode, burbot did not.

A fourth factor may also be involved. Larval parasites may change the behaviour of the infected intermediate host so that it becomes susceptible to predators feeding in one way, but not to those feeding in another way (Holmes and Bethel, 1972; Bethel and Holmes, MS). In that way, two predators feeding on the same intermediate host species could be feeding on different parts of the intermediate host's population, and acquire different parasites. The data presented earlier on sticklebacks taken by pike and trout indicate that these predators are feeding on a selected part of the stickleback population and get different parasites than surface-feeding birds would get. There is no evidence, however, that pike feed on a different part of the stickleback population or are exposed to different parasites than trout.

VI. PARASITES OF COHO

Fingerling coho salmon (age class II), raised from eggs in the Alberta Government hatchery at Raven Creek, were introduced experimentally into Cold Lake, Alberta, each spring from 1970 through 1972. I was able to study their parasites in 1971, when they were introduced in late June, and in 1972, when they were introduced in late April. Samples of fingerlings (57 in 1971, 23 in 1972, for a total of 80) were examined for metazoan parasites at the time of their release into Cold Lake; no parasites were found.

Very few parasites were found regularly in coho during their first summer in the lake; a few others were found sporadically (Table 16). More species (10) were encountered in the class II coho in 1972 than in 1971 (6), as might be expected from their longer residence in the lake. However, the mean number of individuals per infected fish did not differ significantly between years, and the mean number of species per fish was significantly less in 1972 than in 1971 (Table 16).

Almost all coho examined were infected with *M. salmonis* soon after entering the lake; it was the only parasite found regularly in both years. Populations of *M. salmonis* in the young coho appeared to be fairly similar in the two years through August, but were markedly higher in September and October of 1972, reflecting the considerably larger size of the fish taken in those periods (Table 17), many of which were large precocious males.

The two species of *Ergasilus* were abundant in young coho in 1971, but relatively scarce in 1972 (Table 16), accounting for the difference

Table 16. Comparison of the prevalence and mean intensity (in parentheses) of parasites acquired by coho salmon of age class II

Parasites	1971	1972
Crepidostomum farionus	4.6 (4.0)	4.8 (1.1)
Duphyllobothrium sp.**	0	5.5 (1.3)
Eubothrium spp.*	0	2.8 (2.3)
Proteocephalus spp.*	0	4.8 (7.1)
*Triaenophorus nodulosus***	1.5 (2.0)	4.1 (1.1)
Metechinorhynchus salmonis	100 (37.5)	98.6 (65.2)
*Pomphorhynchus bulbocolli**	9.2 (2.5)	2.1 (1.0)
*Neoechinorhynchus strigosum**	0	1.4 (3.0)
Ergasilus auritus	36.9 (4.9)	7.6 (5.5)
Ergasilus nerkae	93.9 (38.0)	16.6 (7.0)
No. examined[1] (n)	65	145
No. spp. (S)	6	10
Mean no. spp. ($\bar{S}$) (± S.E.)	2.45 (±0.09)	1.5 (±0.06)
Mean no. ind. per infected host ($\bar{N}$) (± S.E.)	75.4 (±5.45)	66.6 (±6.65)

[1] Excluding a total of 80 coho examined in both years before releasing, all were negative.

*Immature.

**Larval.

Table 17. The seasonal prevalence and mean intensity (in parentheses) of common parasites acquired by age class II coho salmon in 1971 and 1972. The coho were introduced into Cold Lake in late June, 1971 and late April, 1972. Values for S, $\bar{S}$ and $\bar{N}$ are for the entire parasite fauna.

Parasites		June	July	August	September	October
Metechinorhynchus salmonis	1971		100(26.5)	100(31.8)	100(39.3)	100(105)
	1972	87.5(35.7)	97.4(20.1)	100(38.4)	100(187.2)	100(243.5)
Ergasilus auritus	1971		25(1)	46.5(5.9)	7.1(10)	75(6)
	1972	12.5(40)	0	14.3(2.1)	0	0
Ergasilus nerkae	1971		0	100(29.5)	100(52.6)	75(34)
	1972	0	0	34.3(7.0)	0	0
No. examined	1971	0	4	43	14	4
	1972	8	38	70	20	9
Mean fork length (±S.D.)	1971		20.7(±1.5)	22.8(±0.22)	24.8(±0.76)	26.3(±0.65)
	1972	19.9(±1.16)	23.0(±0.44)	26.3(±0.39)	34.6(±0.85)	38.3(±0.6)
S	1971		3	7	5	3
	1972	3	1	8	7	2
$\bar{S}$	1971		1.50	2.65	2.29	2.50
	1972	1.50	0.97	1.79	1.55	1.11
$\bar{N}$±S.E.	1971		29.3(±7.9)	68.3(±5.2)	93.4(±11.3)	135(±42.0)
	1972	69(±26.1)	20.1(±3.1)	41.5(±6.2)	188.0(±20.5)	234.7(±33.1)

in $\bar{S}$ between years. For *E. nerkae*, the decrease in 1972 paralleled a similar reduction in the population of this parasite in cisco, but the population of *E. auritus* in cisco did not decrease in 1972 (Table 11). At least in 1971, *E. nerkae* appeared later, and reached peak populations later, than *E. auritus* (Table 17). This seasonal pattern is similar to that in cisco.

Relatively small numbers of overwintered age class III coho were recaptured, mainly in the fall when they returned to spawn in the Medley River. In general, these overwintered coho harboured more individuals of more species of parasites than did the younger coho (Table 18), including substantial populations of two species, *C. stigmatura* and *P. agubernaculum*, not encountered in the class II coho. Only *E. nerkae* was significantly more abundant in the younger coho. As in the younger coho, their parasite fauna was dominated by *M. salmonis*.

Overwintered coho captured in 1971 had significantly higher $\bar{S}$ and $\bar{N}$ than those captured in 1972 or 1973 (Table 19). The mean intensity of *M. salmonis* in 1971 was almost double that in 1972 or 1973; the same pattern was seen in cisco, but not in whitefish (Table 11). The two ergasilids were abundant in 1971, but sporadic or absent in the other two years. *E. nerkae* showed the same pattern in other hosts, but *E. auritus* (in cisco) did not. Of the other species which showed similar decreasing populations over the three years, the decrease in *C. stigmatura* was noteworthy, since populations of that parasite in whitefish increased over the same period (Table 11).

The general food habits of coho were covered earlier (section V, C). Because of the major differences in the parasite faunas of coho taken in different years, or of different ages, the diets of these groups

Table 18. The prevalence and mean intensity (in parentheses) of parasites acquired by coho salmon of age classes II and III

Parasites	Age class	
	II	III
Discocotyle sagittata	0	1.3 (1.0)
Crepidostomum farionis	4.8 (2.0)	14.1 (2.3)
Cyathocephalus truncatus	0	2.6 (1.0)
Diphyllobothrium sp.**	3.8 (1.4)	7.7 (1.7)
Eubothrium spp.*	1.9 (2.3)	1.3 (12.0)
Proteocephalus spp.*	3.3 (7.1)	2.6 (19.0)
*Triaenophorus nodulosus***	3.3 (1.3)	1.3 (2.0)
Cystidicola stigmatura	0	15.4 (3.1)
Philonema agubernaculum	0	56.4 (19.3)
Metechinorhynchus salmonis	99.1 (57.5)	100 (532.9)
*Pomphorhynchus bulbocolli**	3.8 (2.3)	11.5 (1.2)
*Neoechinorhynchus strigosum**	1.0 (3.0)	0
Ergasilus auritus	16.7 (5.1)	16.7 (10.0)
Ergasilus nerkae	40.5 (29.2)	30.8 (26.7)
No. examined (n)	210	78
No. spp. (S)	10	13
Mean no. spp. ($\bar{S}$) (± S.E.)	1.79 (±0.06)	2.68 (±0.17)
Mean no. ind. per infected host ($\bar{N}$) (± S.E.)	68.1 (±4.88)	555.7 (±44.44)

*Immature.

**Larval.

Table 19. Comparison of the prevalence and mean intensity (in parentheses) of parasites acquired by 3-year old coho recovered in various years

Parasites	1971	1972	1973
Discocotyle sagittata	3.9 (1.0)	0	0
Crepidostomum farionis	30.7 (2.0)	7.7 (2.0)	2.6 (6.0)
Cyathocephalus truncatus	0	0	5.1 (1.0)
Diphyllobothrium sp.**	15.4 (1.8)	0	7.7 (1.7)
Eubothrium spp.*	3.9 (12.0)	0	0
Proteocephalus spp.*	0	0	5.1 (19.0)
Triaenophorus nodulosus **	0	0	2.6 (2.0)
Cystidicola stigmatura	30.8 (3.3)	23.1 (2.7)	5.1 (2.5)
Philonema agubernaculum	69.2 (37.6)	46.2 (2.0)	59.0 (9.7)
Metechinorhynchus salmonis	100 (782.6)	100 (404.4)	100 (407.9)
*Pomphorhynchus bulbocolli**	23.1 (1.1)	15.4 (1.5)	2.6 (2.0)
Ergasilus auritus	46.2 (9.8)	7.7 (13.0)	0
Ergasilus nerkae	92.3 (26.7)	0	0
No. examined (n)	26	13	39
No. spp. (S)	10	6	9
Mean no. spp. ($\bar{S}$) (± S.E.)	4.15 (±0.29)	2.0 (±0.25)	1.92 (±0.13)
Mean no. ind. per infected fish ($\bar{N}$) (±S.E.)	842.4 (±89.4)	407.3 (±94.1)	414.1 (±37.4)

*Immature.

**Larval.

were examined in more detail. Much of the following information comes from Roberts (1975), who studied the food of the coho I examined for parasites.

The major difference in the diets of the age class II coho between 1971 and 1972 appeared to be that a larger proportion had fed on fish and a much lower proportion had fed on insects in 1972 (Table 20). Older coho (age class III) fed even more extensively on fish (Table 20). Both features appear to be a function of size; Roberts (1975) analyzed the diets of class II coho by size (as measured by fork length), and found a decreasing dependence on invertebrates and an increasing dependence on fish as the coho increased in size.

DISCUSSION

When fish introduced into a new environment have been raised from eggs in a hatchery, such as the coho were, they do not transfer parasites characteristic of their native environment, although they may transfer new parasites, particularly protozoans or ectoparasites, acquired in the hatchery (Ivasik, Kulakovskaya and Vorona, 1969; Malmberg, 1972; Wootten, 1972). None of the coho examined before release had observable infections, suggesting that no new metazoan parasites, at least, were introduced. However, the very small numbers of P. *agubernaculum* in cisco did not appear to be sufficient to produce the heavy infections in over-wintered coho, suggesting the possibility that P. *agubernaculum* may have been introduced, in a cryptic early migratory stage, with the coho.

The young coho introduced into Cold Lake fed vigorously on insects, then later on fish, especially ninespine sticklebacks; the latter are a

Table 20. The prevalence of food in 1971 and 1972 age class II coho, age class II coho of both years, and age class III coho

	1971	1972	Combined years	
	II*	II	II	III
Whitefish	0	8.3	5.7	0
Cisco	4	1.9	2.5	46.4
Cyprinids	0	1.9	1.3	3.6
Walleye	0	1.0	0.6	0
Stickleback	30	38.0	35.4	32.1
Total Fish	34	51.1	45.5	82.1
Mysis relicta	2	0	0.6	0
Pontoporeia affinis	2	0	0.6	7.1
Gammarus lacustris	2	0	0.6	0
Total Amphipods	4	0	1.2	7.1
Total Crustaceans	6	0	1.8	7.1
Ephemeroptera	0	0	0	7.1
Odonata	16	0	5.1	0
Hemiptera	4	0	1.3	10.7
Trichoptera	74	54.6	60.8	7.1
Coleoptera	22	0	6.9	7.1
Diptera	18	2.8	7.6	0
Total Insects	134	57.4	81.7	32.0
Glossiphonidae	0	1.0	0.6	0
No. examined (n)	65	145	210	78
No. with food	50	108	158	28
No. food items (S(F))	10	8	14	8
Mean no. food items ($\overline{S}$(F))	2.3	1.2	1.5	1.1
(±S.D.)	(±0.14)	(±0.04)	(±0.07)	(±0.08)

* age class.

transport host for *M. salmonis*. The high prevalence and mean intensity of *M. salmonis*, and differences in these parameters in different years or age classes, were directly due to this vigorous feeding on sticklebacks. In contrast, kokanee (*Oncorhynchus nerka*) introduced into Lake Huron, which fed mainly on invertebrates and did not prey on other fishes (Collins, 1971), had much lower intensities of *M. salmonis* (Collins and Dechtiar, 1974) than did the coho in my study.

However, the high intensity of ergasilids could not be due to vigorous feeding by coho; it is probably a reflection of the behaviour of the young coho, which feed extensively in the upper surface waters of the lake in the early evening (Roberts, 1975). The recovery of large numbers of aerial insects from the stomachs of coho further strengthened this observation of preference for the upper surface. This preference, combined with the tendency of the nauplii of *Ergasilus* spp. to move to the surface at night (Bauer, 1959), produced a high potential for infection with ergasilids.

A greater number of parasite species were recovered from coho introduced in April, 1972, than those introduced in June, 1971; further, overwintered coho acquired more parasite species than those which had not overwintered, suggesting that the length of residence was an important factor.

Salmonid fish dominated the community of fish in Cold Lake and the parasite community was similarly dominated by those characteristic of salmonid fish. The parasites acquired by the introduced coho reflected that situation; 11 of the 14 species were primarily parasites of salmonids. The most abundant parasites were *P. agubernaculum*, *M. salmonis*, *E. auritus* and *E. nerkae*, all parasites of salmonids. Only three parasite species

(*T. nodulosus*, *P. bulbocolli* and *N. strigosum*) were acquired from non-salmonid fish, and of these, only *P. bulbocolli* was reasonably abundant.

There appear to be only two other reports of parasites in introduced coho. Klein and Fennel (1969) recovered only two species of parasites (*Crepidostomum farionis*, a parasite of salmonids, and *Proteocephalus* sp., which cannot be allocated to a particular host group) in 3 of 103 individual coho from Parvin Lake, and none from Granby Reservoir, Colorado. Both bodies of water have a fairly large number of species of salmonid fishes (mostly introduced), but only in Parvin Lake did salmonid fishes, mainly rainbow trout and splake (*Salvelinus fontinalis* X *S. namaycush* hybrid), dominate the community.

Becker and Brunson (1968) reported plerocercoids of *Proteocephalus ambloplitis* in 9 of 243 young coho, but none of 20 two-year old coho planted in Goodwin Lake, Washington, which has a resident population of largemouth bass, *Micropterus salmoides*. They did not mention any other parasites.

Kokanee were introduced into Lake Huron, which has a predominantly non-salmonid fish community (Bangham, 1955; Collins and Dechtiar, 1974). A large proportion of non-salmonid fishes were gill-netted along with the introduced kokanee, suggesting a close association (Collins and Dechtiar, 1974). Only 8 out of 18 parasite species recovered from the kokanee were salmonid fish parasites. However, a large proportion were infected with infected with *M. salmonis*, *Echinorhynchus leidyi* and *C. stigmatura*, all of which were commonly found in salmonid fishes.

Wootten (1973) examined rainbow trout and brown trout introduced as adults into Henningfield Reservoir, Essex, which had no salmonid fish. They harboured 11 and 13 parasite species respectively, including

D. sagittata and *Eubothrium crassum*, salmonid parasites which were probably introduced with the trout. Most of the parasites acquired were ectoparasites or larval parasites which culminated their life cycle in piscivorous birds. Very few endoparasites were acquired.

Some of the parasites acquired by coho are known to be pathogenic to other hosts. Heavy infections of *E. salvelini* apparently have no effect on lake trout, but small numbers of young tapeworms were found to have detrimental effects on growth and swimming performance in infected juvenile sockeye salmon (*O. nerka*), which resulted in an increased susceptibility to predators (Smith, 1973). The parasite is primarily one of fry or smolt in sockeye salmon (Boyce, 1974; Smith, 1973), and Boyce showed that susceptibility to infection decreased rapidly as the young salmon grew. No evidence of damage was found in the few coho infected with *Eubothrium* plerocercoids. The coho may have already grown past the stage most susceptible to infection when introduced.

In brown trout infected with *C. truncatus*, the mucosal layer of infected pyloric caeca was destroyed, with fibrous tissues formed at the site of attachment; in older infections, this reaction caused the fusion of neighbouring pyloric caeca (Awachie, 1966; Halvorsen and Macdonald, 1972). Such thickened fibrous tissues were observed in heavily infected whitefish, but few coho were infected with *C. truncatus* and no observations were made on the possible effects on the new host.

Infection of *Ergasilus* on the gill filaments may cause a strong reaction from the host, resulting in the destruction of the gill epithelium and a fusion of gill lamellae (Bauer, 1959; Kabata, 1970; Rogers, 1969). Einszporn-Orecka (1970) showed that *Tinca tinca* infected with *E. sieboldi* had a general low blood protein and a decrease in erythrocytes which could cause anaemia. He considered that heavy infections with *E. sieboldi* could cause the death of fishes.

No visible reaction was observed in coho heavily infected with *E. auritus* and *E. nerkae*. However, no histological examination of the infected regions were made.

Simon and Simon (1936) observed some pathological changes, particularly in the gonads, in mountain whitefish, eastern brown trout and rainbow trout infected with *P. agubernaculum*. In heavily infected coho, large numbers of *P. agubernaculum* were found between the pyloric caeca and were accompanied by thread-like adhesions between adjacent pyloric caeca or to the coelomic wall.

Although no histological sections of intestines heavily infected with *M. salmonis* were examined, there was an obvious tissue thickening at the site of proboscis attachment in the posterior region of heavily infected whitefish. The heavy infection of *M. salmonis* in coho might cause some host reaction.

In view of the fact that infections of *E. salvelini*, *C. truncatus*, *P. agubernaculum*, *M. salmonis*, *E. auritus* and *E. nerkae* do cause pathological reactions in other hosts, these same species, particularly the last four which infected coho heavily (at least in some years), could have had some detrimental effects on the introduced coho. The lack of success of the introduction of coho into Cold Lake might have been due in part to the heavy infections with these parasites.

VII. THE BIOLOGY OF *METECHINORHYNCHUS SALMONIS*

It is obvious that the patterns in the parasite communities were set by the dominant parasites, essentially those of salmonid fishes, and particularly *M. salmonis*, the most dominant parasite. Since *M. salmonis* exerted such a strong influence on the parasite communities, it deserves special attention; its biology is examined in greater detail in this section.

At least some individuals of each species of fish examined in the present study were infected, with high prevalences in whitefish, lake trout, coho, longnose sucker, pike and burbot; stickleback and white-sucker had the lowest prevalence (Table 21). Lake trout (with a mean intensity of 421) and three-year old coho (533), two predators, had very high mean numbers of individuals; ninespine sticklebacks had the least (1.8).

Female *M. salmonis* were arbitrarily assigned to one of three stages of maturation as described by Tedla and Fernando (1970): 1) females with ovarian balls predominant; 2) females with non-shelled acanthors predominant; and 3) females with shelled acanthors predominant (gravid) in the body cavity. Unfixed female acanthocephalans were teased apart and their maturation assessed under a compound microscope. The matur[illegible] preserved acanthocephalans was assessed after dehydration in glacial acetic acid and clearing in creosote (Chubb, 1962).

Gravid females comprised a large proportion (about 50%) of the *M. salmonis* in both cisco and 3-year old coho, a moderate proportion

Table 21. Prevalence, mean intensity, number of females and maturation of *Metechinorhynchus salmonis* in various host species in Cold Lake

	No. exam.	Prevalence	Mean intensity ± S.E.	Total no. female acanthocephalans	% female gravid acanthocephalans
Lake whitefish	836	99.5	170.2 ±5.8	31585	14.2
Cisco	(961)[3]	32.4	8.7 ±0.7	3127	49.6
Lake trout	35	100	420.9 ±39.2	3847	24.3
Coho salmon (II)[1]	210	99.0	57.5 ±5.4	980	20.4
Coho salmon (III)[2]	78	100	532.[illegible] ±43.2	18525	56.9
Walleye	12	66.7	3.0 ±0.4	19	0
Ninespine sticklebacks	1038	19.0	1.8 ±0.1	50	0
Whitesucker	36	8.3	4.0 ±3.0	4	0
Longnose sucker	12	83.3	30.9 ±5.8	77	0
Northern pike	62	83.9	30.6 ±5.8	72	2.8
Burbot	29	100	174.4 ±23.8	1003	1.7

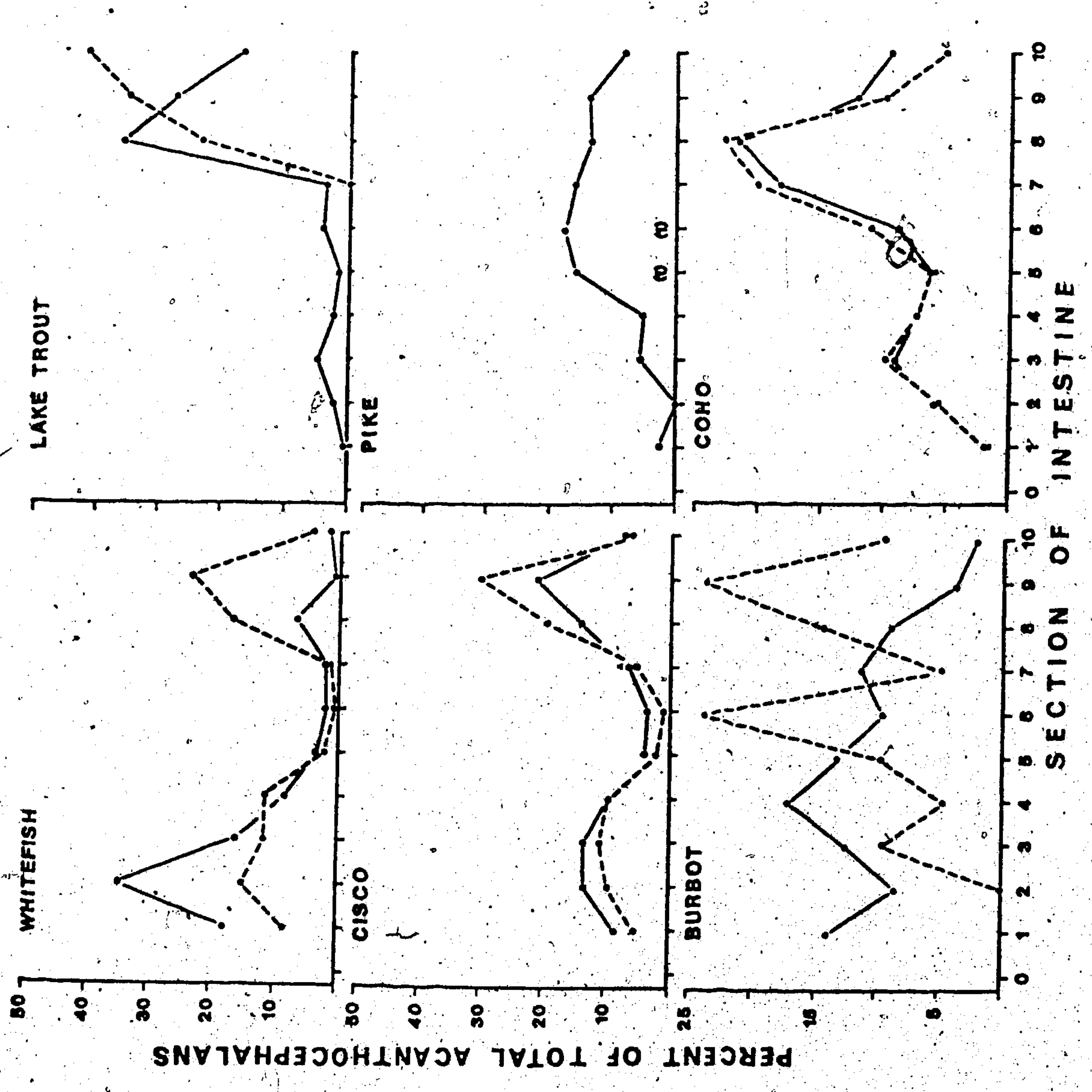
[1] fish introduced in spring and recaptured through fall.
[2] fish overwintered in the lake.
[3] 757 + 204 examined only for *M. salmonis*.

(10-25%) in other salmonids, and a very small proportion (less than 3%) in pike and burbot (Table 21). The majority of the worms in pike and burbot, and all of those recovered from walleye, stickleback, whitesucker and longnose sucker showed some growth, but otherwise little change from excysted cystacanths.

The distribution of *M. salmonis* within the gut of the fish was examined in all fish taken after May, 1973. At necropsy, the intestine was divided into ten sections of equal length, and the number of parasites in each section was determined.

The distributions of *M. salmonis* in the fishes examined are shown in Figure 18. In whitefish, the acanthocephalans were concentrated at the anterior end, where they were found mainly in the pyloric caeca. However, a higher proportion of those in the posterior end were gravid females, so that almost equal proportions of the gravid females were found in the anterior and posterior regions. In cisco, approximately equal numbers of acanthocephalans were found in the anterior (pyloric caeca) and posterior regions, but the gravid females were predominately in the posterior region. In lake trout, the acanthocephalans, and particularly the gravid females, were virtually limited to the posterior third of the intestine. In coho, the acanthocephalans, including the gravid females, were found throughout the intestine, but peak numbers were in the posterior region. In pike, the acanthocephalans were distributed fairly evenly throughout the posterior half of the intestine, but both the two gravid females were found in the mid-intestine. In burbot, they were widely dispersed, with most of the worms in the anterior half of the intestine, although most of the gravid females were in the posterior half.

Figure 18. Intra-intestinal distribution of *Metechinorhynchus salmonis* (as percentage of total number (————)) and gravid female *M. salmonis* (as percentage of total number (--------)) in fishes from Cold Lake, Alberta


PERCENT OF TOTAL ACANTHOCEPHALANS
SECTION OF INTESTINE
WHITEFISH
LAKE TROUT
CISCO
PIKE
BURBOT
COHO
50
40
30
20
10
50
40
30
20
10
25
15
5
0
1
2
3
4
5
6
7
8
9
10

The mean intensity of *M. salmonis* increased considerably, and in a linear fashion, with age in whitefish (Figure 19). Consequently, their maturation and distribution in this species of host were analyzed by age class. The proportion of gravid females reached a peak in age class IV, then declined through age class VIII (Figure 19). Despite the tremendous increase in mean intensity between age classes IV and IX, there was no significant variation in the mean intensity of gravid females among these age classes (overall mean, 11 ± 0.74).

The intraintestinal distribution of the *M. salmonis* changed with age, gradually shifting from a pattern with a high peak at the posterior region of the gut (essentially similar to the pattern in cisco) in young whitefish to one with a high peak in the anterior region of the intestine in the old whitefish (Figure 20). Although the proportion of the acanthocephalans in the posterior 30% of the intestine declined with age, the mean number of acanthocephalans in that portion of the intestine did not vary significantly in age classes IV through IX. The shift in distribution was due to the establishment of additional acanthocephalans in the anterior part of the intestine, and suggested that availability of space, particularly the size of the opening and the length of the pyloric caeca, was important for attachment.

The patterns of distribution of gravid female *M. salmonis* were similar to those of the total acanthocephalans, with a high peak at the posterior region of the intestine in young whitefish and a high peak at the anterior region of the intestine in old whitefish (Figure 21). The mean numbers of gravid female acanthocephalans in the last 30% of the intestine did not vary significantly in age classes IV through IX, but the number in the anterior 30% did increase significantly. These

Figure 19. The abundance (————) and maturation (--------) of *Metechinorhynchus salmonis* in whitefish of age classes II to IX

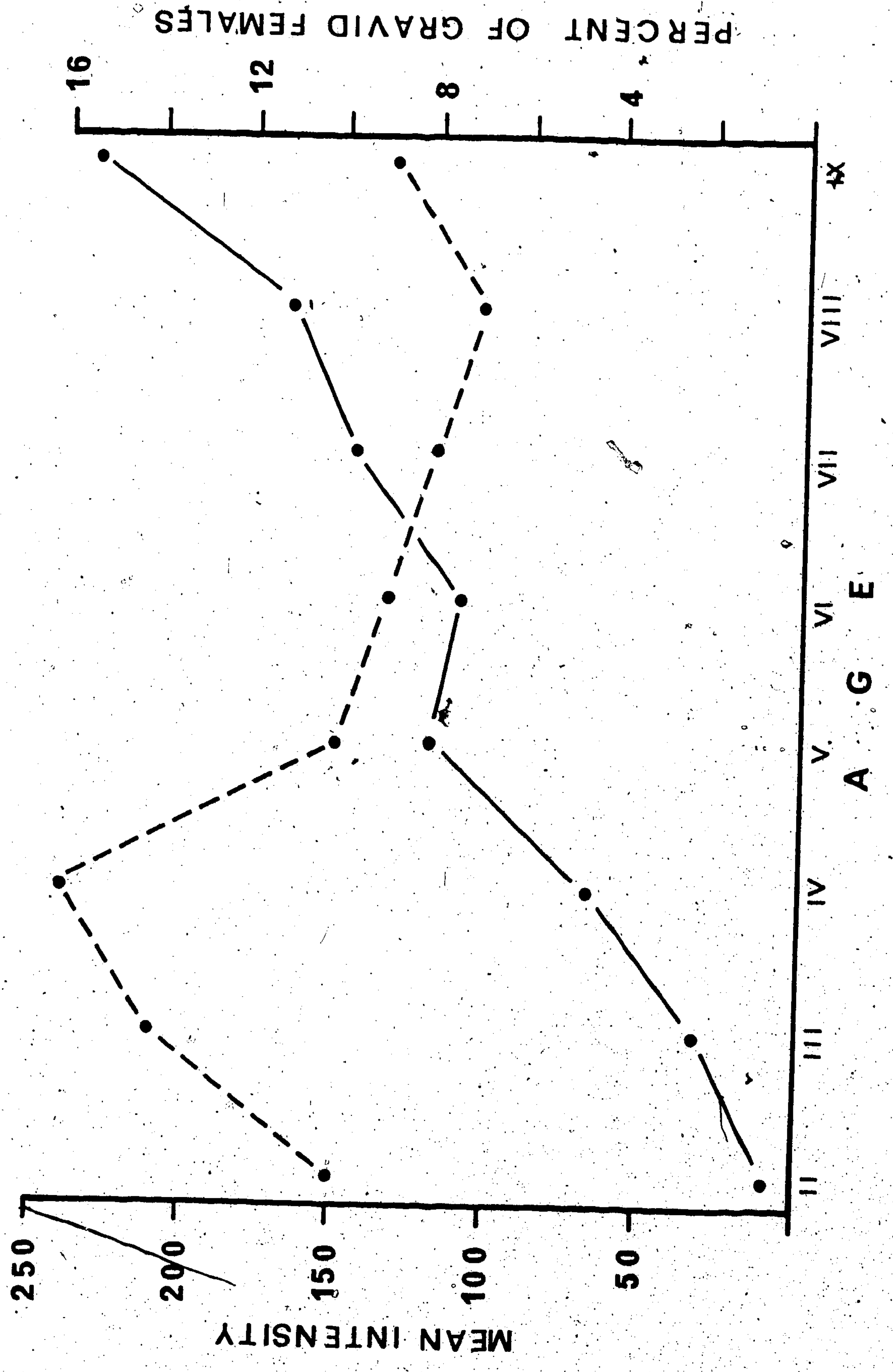

MEAN INTENSITY
250
200
150
100
50
PERCENT OF GRAVID FEMALES
16
12
8
4
AGE
II
III
IV
V
VI
VII
VIII
IX

Figure 20. Distribution of *Metechinorhynchus salmonis* in the intestine of lake whitefish of age classes II, IV, VI and IX

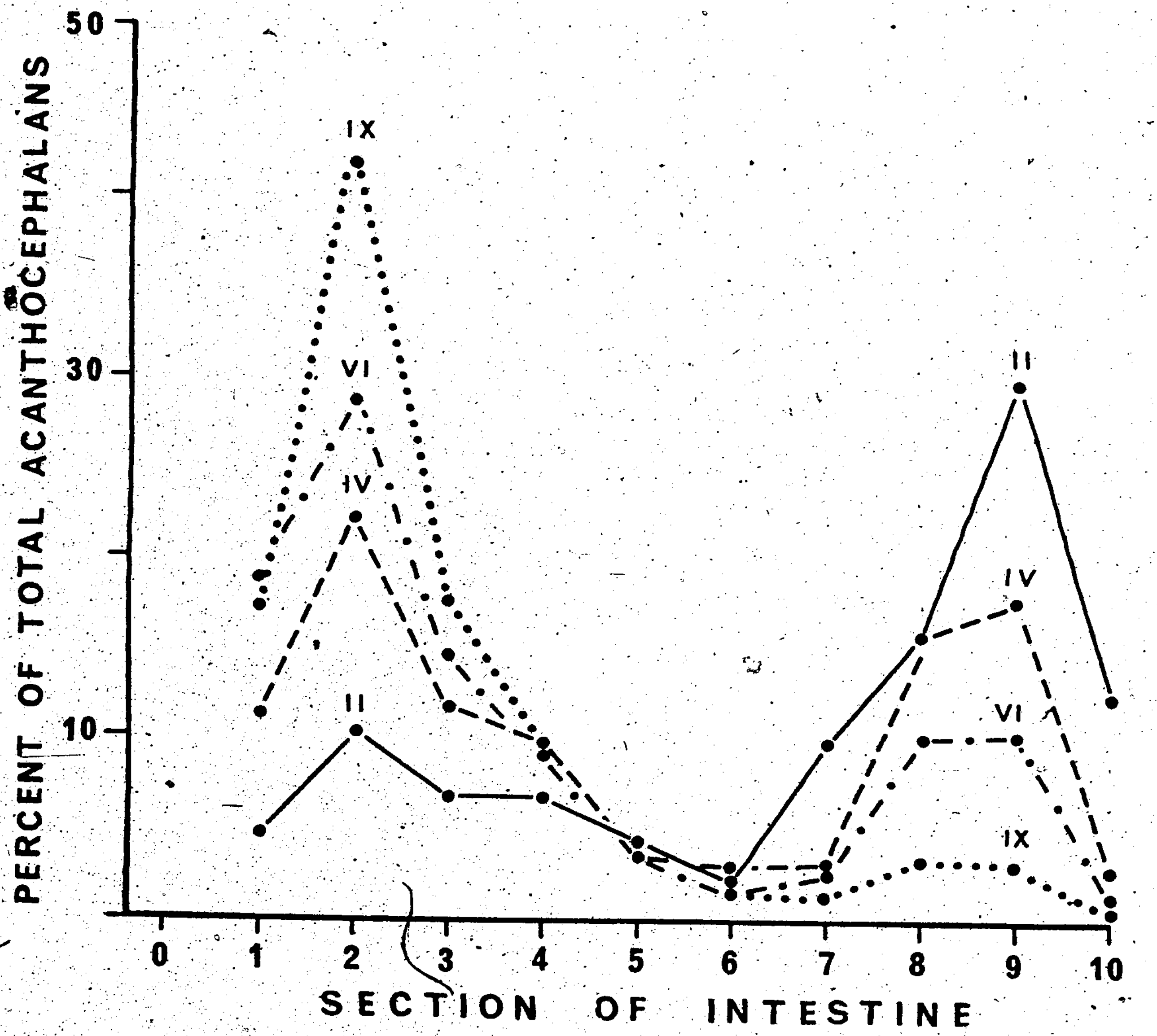
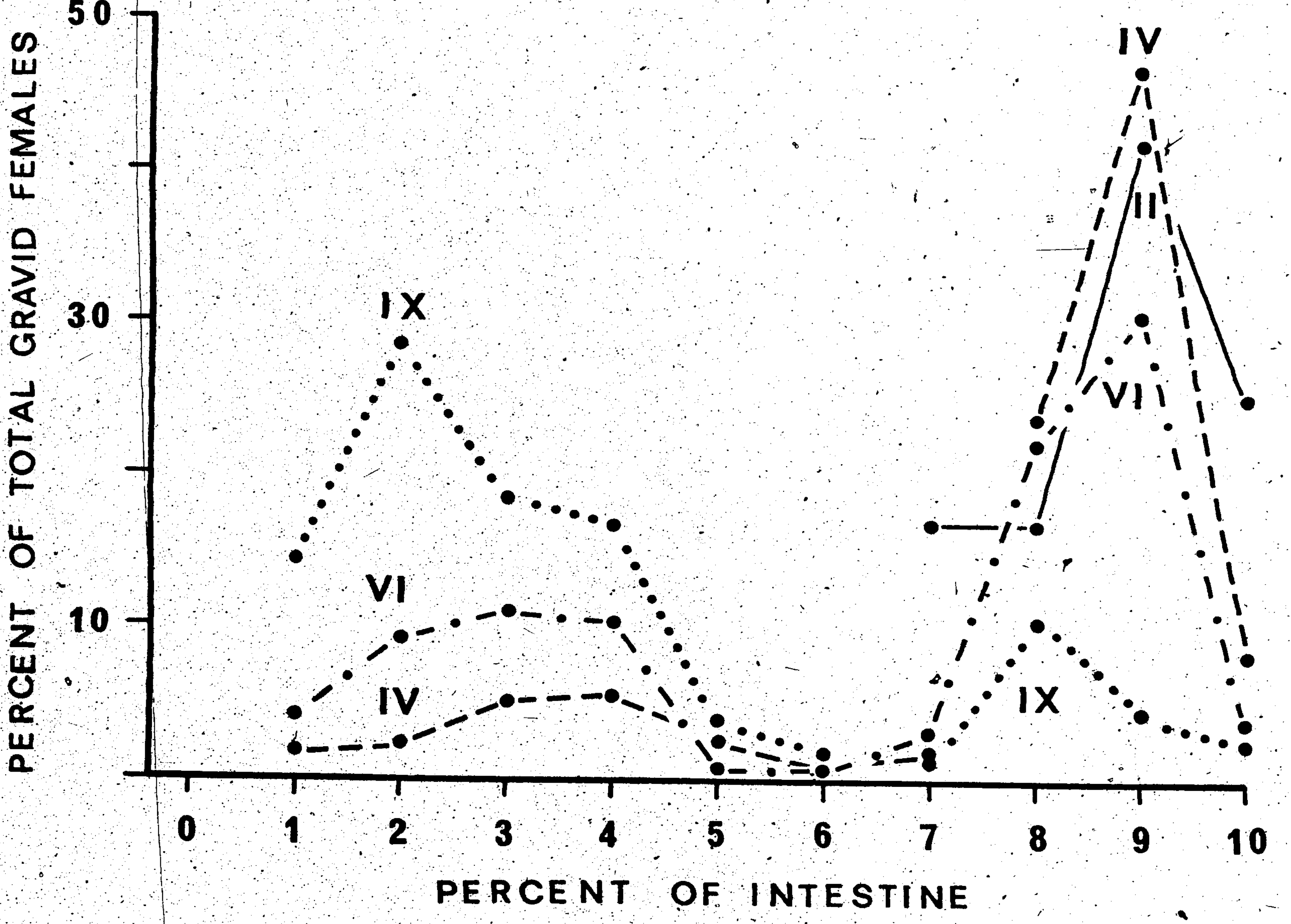

50
30
10
PERCENT OF TOTAL ACANTHOCEPHALANS
0
1
2
3
4
5
6
7
8
9
10
SECTION OF INTESTINE
IX
VI
IV
II
II
IV
VI
IX

Figure 21. Distribution of gravid female *Metechinorhynchus salmonis* in the intestine of lake whitefish of age classes II, IV, VI and IX


PERCENT OF TOTAL GRAVID FEMALES
50
30
10
PERCENT OF INTESTINE
0
1
2
3
4
5
6
7
8
9
10
IX
VI
IV
IV
II
VI
IX

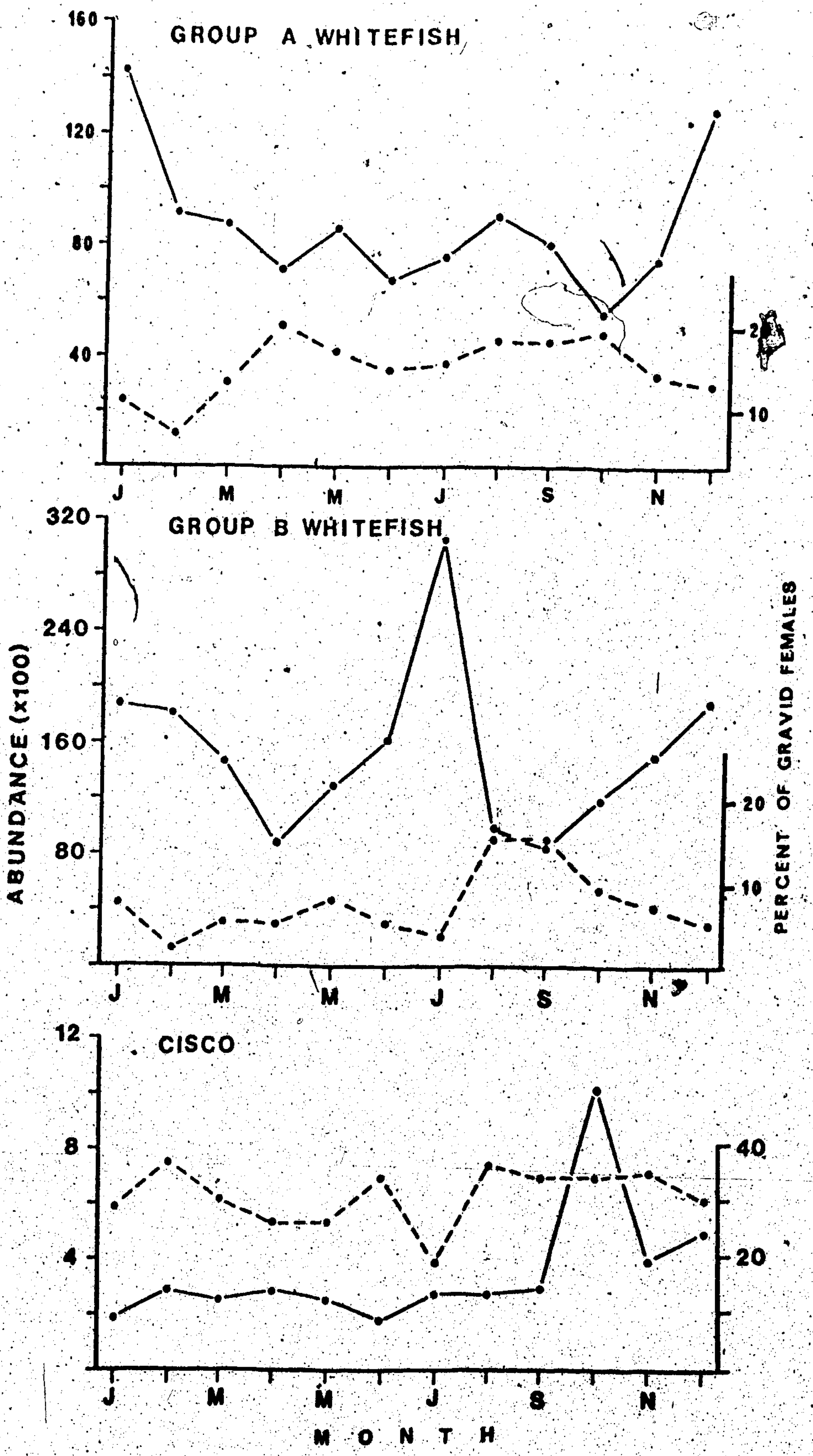
observations suggested that the acanthocephalans did not move down the intestine for maturation, as suggested earlier by Awachie (1966a) and Tedla and Fernando (1970).

The seasonal patterns of abundance of *M. salmonis* have been presented earlier. In brief, peak abundances were reached in early winter in both groups of whitefish and in cisco. Group B whitefish showed a second, late summer, peak, which was less obvious in the Group A whitefish and absent in cisco.

Gravid female *M. salmonis* were found in the intestine throughout the year. In whitefish, there was no obvious seasonal pattern in the proportion of gravid females in the population (Figure 22); rather, the percent gravid females showed a general inverse relationship to the total number of acanthocephalans in the same samples (Group A whitefish: $r = -0.55$, $t = 2.06$, $P < 0.1$; Group B whitefish: $r = -0.64$, $t = 2.64$, $P < 0.05$). The numbers of gravid females did not vary significantly among months. In cisco, neither the percentage of gravid females nor the number of gravid females varied significantly among months.

The preceding analyses suggest that the maturation of female *M. salmonis* is affected by the number of acanthocephalans present and the age (or, more probably, the size) of the fish, and that the effects of these factors differ among species of hosts. The lower percentages of gravid females in whitefish and trout, which also harboured significant numbers of mature cestodes, than in cisco and coho, which had few (or small, immature) cestodes, suggest that the number of cestodes also may be affecting maturation. Consequently, data on individual fish of each of these four species of salmonids were examined to determine the relationships between maturation of *M. salmonis* (measured by the number of gravid

Figure 22. Seasonal patterns in the abundance (————) and maturation (--------) of *Metechinorhynchus salmonis* in whitefish and cisco


GROUP A WHITEFISH
160
120
80
40
20
10
J
M
M
J
S
N
GROUP B WHITEFISH
320
240
160
80
20
10
J
M
M
J
S
N
CISCO
12
8
4
40
20
J
M
M
J
S
N
M O N T H
ABUNDANCE (x100)
PERCENT OF GRAVID FEMALES

females (G) and by the percentage of gravid females (PG)) and the total number of acanthocephalans (A), the number of cestodes (C), and the size of the host (measured by fork length (FL) in trout, by the length of intestine (IL) in the others).

In whitefish, all variables were significantly interrelated (Table 22). The number of gravid females (G_W) was positively related to all three independent variables. However, the stepwise multiple regression analysis indicated that the number of acanthocephalans was the most important independent variable, that the length of intestine also explained a significant amount of the variance, but that the number of cestodes did not (Table 23). The multiple regression equation is:

$$G_W = 0.015 + 0.035A_W + 0.031IL_W$$

which accounted for 11.2% of the variance ($P < 0.001$).

The percent of gravid females in whitefish (PG_W) was negatively related to the other variables (Table 22), but only the number of acanthocephalans explained a significant amount of the variance (Table 23). The regression equation is:

$$PG_W = 15.71 - 0.027A_W$$

and accounted for only 6.1% of the variance ($P < 0.001$).

In cisco, there were no significant relationships between the number of acanthocephalans, the number of cestodes, and the length of the intestine. The number of gravid females (G_C) was positively related to the independent variables A_C and IL_C (Table 22) and the stepwise multiple regression analysis indicated that each explained a significant amount of variance (Table 23). The number of acanthocephalans was an extremely

Table 22. Correlation coefficients between variables; values above the diagonal are for numbers of gravid females, those below the diagonal for percent of gravid females. The symbols are explained in the text

	Whitefish (n=379) PG	A	C	IL	Cisco (n=396) PG	A	C	IL
G	—	0.32**	0.12*	0.24**	—	0.86**	-0.05	0.13**
A	-0.25**	—	0.59**	0.47**	-0.01	—	-0.01	0.07
C	-0.16**	0.59**	—	0.24**	-0.10*	-0.01	—	-0.02
IL	-0.10*	0.47**	0.24**	—	0.15***	0.07	-0.02	—

	Trout (n=11) PG	A	C	FL
G	—	0.54	0.19	0.48
A	-0.25	—	0.37	0.63
C	-0.35	0.3[illegible]	[illegible]	0.02
FL	0.18	0.6[illegible]	[illegible]	—

	Coho (n=36) PG	A	IL
G	—	0.84**	0.09
A	-0.04	—	0.35*
IL	-0.27	0.35*	—

* P<0.05

** P<0.001

Table 23. The percent of the variance in the number of gravid females and the percentage of gravid females which are explained by the independent variables in the stepwise multiple regression

Variable	Whitefish	Cisco	Trout	Coho
Number of gravid females(G)				
A	10.0***	73.1***	29.0	69.2***
C	0.6	0.2	0	N/A
IL/FL	1.2*	0.5**	0.3	4.4**
Percent of gravid females(PG)				
A	6.1***	0	11.8	7.5
C	0	0.9	12.1	N/A
IL/FL	0	2.3***	3.4	0.3

\+ P<0.10
* P<0.05
** P<0.01
*** P<0.001

important independent variable, explaining almost three-fourths of the variance. The multiple regression equation is:

$$G_C = -3.643 + 0.311A_C + 0.035IL_C$$

which accounted for 73.6% of the variance ($P < 0.001$).

The percent of gravid females in cisco (PG_C) was significantly negatively related to the number of cestodes and significantly positively related to the length of the intestine (Table 22). The length of intestine explained a significant amount of variance and the variance explained by the number of cestodes was of borderline significance ($P < 0.1$). The regression equation is:

$$PG_C = -1.396 + 0.432IL_C - 0.318C_C$$

but it accounted for only 2.3% of the variance ($P < 0.001$).

In lake trout, the correlation coefficients between each pair of variables (except C and FL) were relatively high, but not statistically significant, probably due to the very small sample size (Table 22). The number of gravid females (G_T) was positively related to all three independent variables. The stepwise multiple regression analysis indicated that the number of acanthocephalans was the most important independent variable, though not statistically significant, and that the other variables were of little importance (Table 23). The regression equation is:

$$G_T = 38.55 + 0.058A_T$$

which accounted for 29% of the variance ($P < 0.1$).

The percent of gravid females in trout (PG_T) was negatively related to the numbers of acanthocephalans and of cestodes, but positively related to the size of the fish (Table 22). Each variable explained a proportion of the variance greater than proportions that were significant in other analyses, but, probably because of the small sample size, none were statistically significant (Table 23). The regression equation is:

$$PG_T = -6.353 - 0.075C_T + 0.06FL_T - 0.02A_T;$$

it accounted for 27.3% of the variance, but was not statistically significant ($P > 0.1$).

In coho, the number of cestodes was very small, so that variable was not included in this analysis. The number of gravid females was positively related to the total number of acanthocephalans, which was positively related to the length of intestine (Table 22). The stepwise multiple regression analysis indicated that the number of acanthocephalans was the most important independent variable, explaining over two-thirds of the variance, and that the length of intestine also explained a significant amount of the variance, but was negatively related to the number of gravid females (Table 23). The multiple regression equation is:

$$G_s = 14.99 + 0.432A_s - 0.747IL_s$$

and accounted for 73.6% of the variance ($P < 0.001$).

The percent of gravid females in coho (PG_s) was not significantly related to the other variables (Table 22). Neither the number of acanthocephalans nor the length of intestine explained a significant amount of the variance. Together, they only accounted for 7.8% of the variance ($P > 0.1$).

DISCUSSION

There are several apparent reasons for the dominant position of *M. salmonis* in the Cold Lake ecosystem. First, *M. salmonis* is a parasite of the salmonids, which dominate the community of fishes. As pointed out earlier, the parasites of salmonids generally dominated the community of parasites.

Second, individual species of acanthocephalans of fish are frequently found in a wide variety of fish (Hoffman, 1967; Petrochenko, 1971). *Metechinorhynchus salmonis* is no exception to this wide host specificity; in the present study, all 10 species of fishes were infected.

Third, there are alternate ways of reaching the fish hosts. The basic life cycle of *M. salmonis* is through *P. affinis*, the intermediate host. The amphipod formed a major part of the diet of whitefish and burbot; in each, the acanthocephalans dominated the parasite community. Amphipods (in Cold Lake, probably *P. affinis*, as deduced from the heavy infections with *M. salmonis*) formed a significant portion of the diet in longnose suckers (Scott and Crossman, 1973), and lesser portions of the diets of cisco and probably of whitesuckers and sticklebacks.

However, the large numbers of *M. salmonis* in trout and coho, which eat few, if any, *P. affinis*, suggest a second route of infection, using sticklebacks, cisco and probably young whitefish as transport hosts. The use of such transport hosts is well established for other acanthocephalans of fish (Petrochenko, 1971). Cisco and particularly sticklebacks formed significant portions of the diets of the predatory fishes in Cold Lake.

Although all fish species examined were found infected with *M. salmonis*, gravid female acanthocephalans were found only in salmonid fishes: whitefish, cisco, trout and coho. The small number of gravid females in pike and burbot might be due to a direct transfer from feeding on infected cisco, since Hnath (1969) has shown that mature *M. salmonis* from coho could survive, for up to 12 weeks, when transferred to brook trout.

To illustrate the relative importance of the alternate life cycle pathways, and the relative importances of the various definitive hosts, I have devised a model of the circulation of *M. salmonis* in the community of fishes in Cold Lake (Figure 23). It must be emphasized that flow rates were not measured in this study. Instead, they were deduced from a static picture of the distribution of *M. salmonis* in the various species of fishes.

The model is based on data on the abundance (prevalence times mean intensity) and percent of gravid females in each of the ten species of fishes examined. The figure for the abundance in each host species was multiplied by the weighting factor (see p. 16 for assumptions implicit in the derivation of that factor) to account for the relative population size of that host, then divided by the sum of the products for all ten fishes to give a first approximation of the proportion of the *M. salmonis* population in that host species (PP_1 in Table 24).

In previous sections, I have shown that populations of *M. salmonis* in whitefish and cisco vary significantly with season and age.

Figure 23. The relative flow rates of *Metechinorhynchus salmonis* in a community of fishes in Cold Lake, Alberta. The solid arrows indicate flow from the intermediate host, *P. affinis*, to various fishes, either directly or through transport hosts (arrows leading from ninespine sticklebacks and cisco). The double arrows indicate flow of eggs from definitive hosts to the intermediate host. Values on the arrows indicate the proportional value of that flow. Values under each fish host are the proportion of the population of *M. salmonis* in that host, followed by percentage of gravid females. See text for detailed explanation.

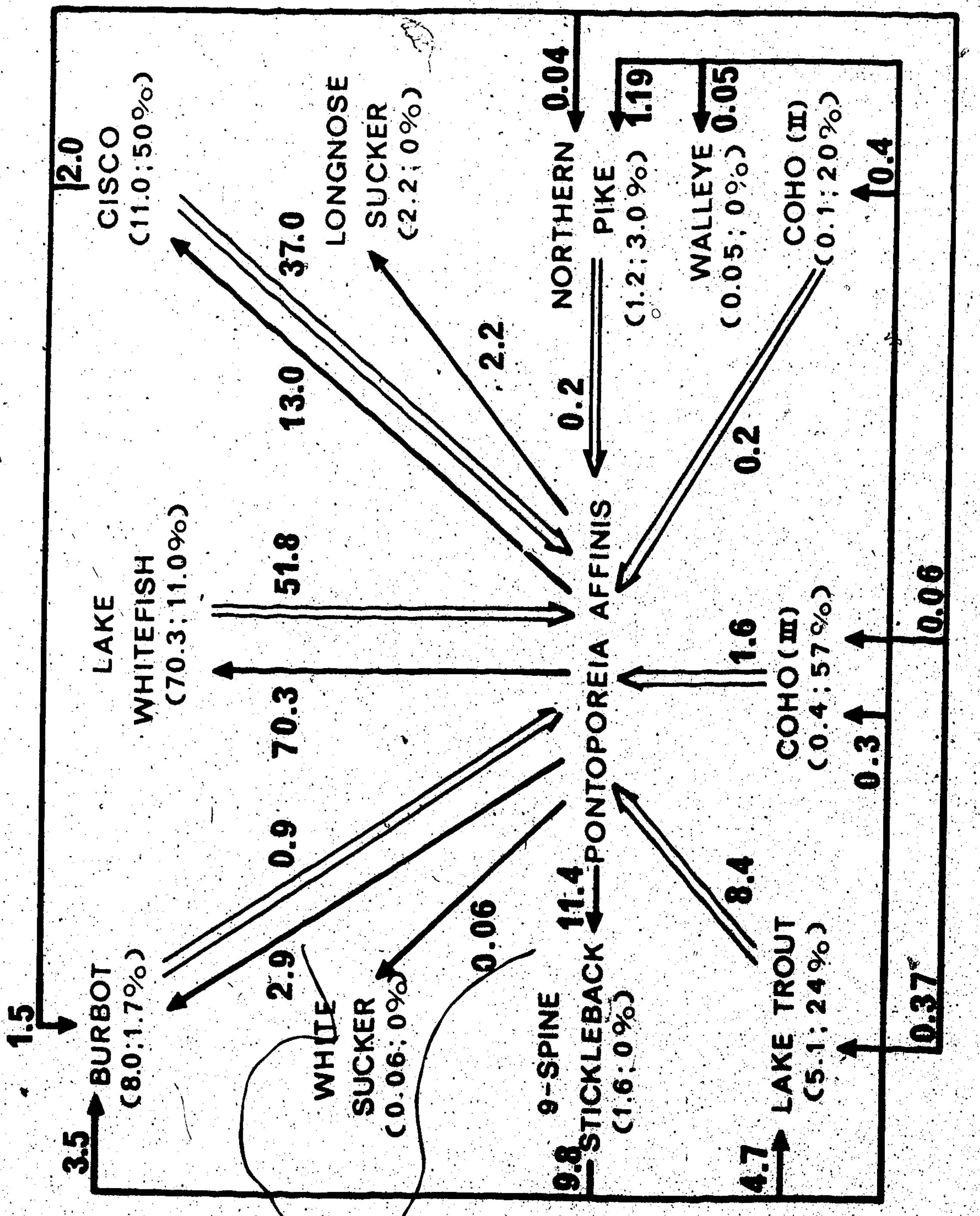

CISCO (11.0; 50%)
LONGNOSE SUCKER (2.2; 0%)
NORTHERN PIKE (1.2; 3.0%)
WALLEYE (0.05; 0%)
COHO (II) (0.1; 20%)
LAKE WHITEFISH (70.3; 11.0%)
PONTOPOREIA AFFINIS
COHO (III) (0.4; 57%)
BURBOT (8.0; 1.7%)
WHITE SUCKER (0.06; 0%)
9-SPINE STICKLEBACK (1.6; 0%)
LAKE TROUT (5.1; 24%)
2.0
37.0
13.0
2.2
0.04
1.19
0.05
0.4
0.2
0.2
51.8
70.3
1.6
0.06
0.3
0.9
2.9
0.06
11.4
8.4
1.5
3.5
9.8
4.7
0.37

Table 24. The proportion of acanthocephalan populations, percent gravid females and proportion of output of eggs in various species of fish, Cold Lake, Alberta

	Abundance	Weighting factor	Unadj.	Adjusted for age, season			Unadj.	Adjusted for age, season			Unadj.	Adjusted for age, season		
			PP_1*	PP_2	PP_3	PP_4	PM_1**	PM_2	PM_3	PM_4	PE_1***	PE_2	PE_3	PE_4
Whitefish	16934.9	28.5	90.2	74.6	70.3	62.8	14.2	11.2	11	10.7	80.9	56.2	51.8	44.6
Cisco	281.9	100	5.3	10.3	11.0	12.3	50	50	50	50	16.9	34.6	37.0	40.6
Lake Trout	42090	0.16	1.3	4.2	5.1	6.9	24				1.9	6.8	8.4	11.1
Coho (II)	5712.3	0.03	0.03	0.1	0.1	0.2	20				0.04	0.2	0.2	0.2
Coho (III)	53290	0.01	0.1	0.3	0.4	0.5	57				0.4	1.3	1.6	2.1
Pike	2567.3	0.6	0.3	1.0	1.2	1.6	3.0				0.05	0.2	0.2	0.3
Whitesucker	33.2	2.18	0.01	0.05	0.06	0.07	0				0	0	0	0
Longnose Sucker	2574	1.1	0.5	1.8	2.2	2.9	0				0	0	0	0
Burbot	17440	0.6	2.0	6.5	8.0	10.7	1.7				0.2	0.7	0.9	1.2
Stickleback	34.2	60	0.4	1.3	1.6	2.1	0				0	0	0	0
Walleye	200.1	0.3	0.01	0.04	0.05	0.06	0				0	0	0	0

* Proportional acanthocephalan population
** Percent gravid female
*** Percent of eggs produced
Subscripts indicate: 1 - unadjusted; 2 - mortality rate at 50%; 3 - mortality rate at 61%; 4 - mortality rate at 72%.

Abundances in these hosts were therefore corrected to account for this variance. The derivation of a seasonal correction factor will be illustrated for Group A whitefish. Since this group contained two age classes, collected in different numbers, I corrected for age effects within this group by calculating a weighted mean (abundance in age IV times the number of age IV fish examined, plus abundance in age V times the number of age V fish, divided by the total of age IV and V fish). The mean of the monthly abundances was divided by this weighted mean to give a correction factor of 0.94, which was used to adjust the abundances (from Appendix IV) of all immature whitefish (age classes II-VI). Similarly, a correction factor calculated for Group B whitefish (1.07) was used to adjust the abundances of mature whitefish (age classes VII-X). A single correction factor (1.12) was calculated and used (on data in Appendix VI) for cisco.

Correction for seasonal variation in abundance of *M. salmonis* in coho was difficult. Coho grew rapidly, and acquired increasing populations of *M. salmonis*, during the summer. My collections were biased towards these larger fish. The uncorrected mean overestimated the abundance of *M. salmonis* in young coho during the summer, but underestimated the abundance during the fall and winter. Since there was no evidence in my data of a seasonal "spawning period" such as that shown for *M. salmonis* in Lake Ontario by Tedla and Fernando (1970), I assume that:

1. Transmission of *M. salmonis* to *P. affinis* may occur throughout the year.

The uncorrected abundance for coho would therefore be as good as any other estimate.

In order to correct for the variation due to age, two factors had to be taken into account, the abundance of *M. salmonis* in each age class, and the relative abundance of host fish in each age class. Seasonally corrected values determined above were used for the former. The latter was calculated by applying an estimate of the annual mortality rate to a hypothetical cohort of 100 class II whitefish (or class I cisco), then calculating the proportions of each age class in the total population.

The mortality rate in Cold Lake was estimated by the differences in total numbers of fish examined in age classes VIII (240), IX (130), and X (19). The reduction between age classes VIII and IX suggested a mortality rate of approximately 50%, the reduction between IX and X a rate of approximately 72%, and that between VIII and X a rate of approximately 61%. The last was very close to the mortality rate estimated by Kennedy (1953) for whitefish in Great Slave Lake, N.W.T., and has been used in the model. A similar mortality rate was assumed for cisco.

The corrected abundance of *M. salmonis* in whitefish (or cisco) was the sum of the products of the seasonally adjusted abundance in each age class multiplied by the proportion of the fish in that age class. These values were used to recalculate the proportion of the *M. salmonis* in each host species (PP_3 in Table 24 and the first value in parenthesis in Figure 23). Proportional populations of *M. salmonis* calculated using the other mortality rates are shown in Table 24.

The input of *M. salmonis* to each host species was initially considered to be equivalent to the proportional population in that species. This assumes that:

2. A *M. salmonis* ingested by any host has the same probability of becoming established, and therefore, that
3. The rate of ingestion of *M. salmonis* by each host species is proportional to the population in that host.

Since there are alternate ways of reaching the fish hosts, the input to each host species had to be apportioned to each of these ways, according to the food habits of the host species. Whitefish, cisco, both species of suckers and sticklebacks did not feed on fish (the small numbers taken by whitefish or cisco are negligible), therefore all input to these species was assumed to be directly from *P. affinis*. Walleye fed only on sticklebacks; all input to walleye was assumed to be by this route. Lake trout and pike did not feed on *P. affinis*, and coho fed on them to a negligible extent, but all fed on both cisco and sticklebacks; the input to each was apportioned to each transport host in proportion to the total number of each forage fish eaten by the predators examined times the abundance of *M. salmonis* in that species of forage fish. This assumes that:

4. The probability of becoming established is the same for a *M. salmonis* ingested in *P. affinis* or in a transport host.

Burbot fed on *P. affinis* and on both transport hosts: *P. affinis* made up 37.5% of the total occurrences of *P. affinis* and fish in the diet, therefore 37.5% of the input of *M. salmonis* to burbot was assumed to be through the amphipod. The remainder of the input was apportioned as above. The input of *M. salmonis* to various predators calculated using the other mortality rates is shown in Table 25.

For each of the two transport hosts, the inputs through that

Table 25. The relative flow rates of *Metechinorhynchus salmonis* by alternate routes to various predators

	Unadjusted	Adjusted survival rate of		
		.5	.39	.28
Trout	RF_1	RF_2	RF_3	RF_4
Sticklebacks	1.2	3.89	4.73	6.4
Cisco	0.09	0.31	0.37	0.5
Pike				
Sticklebacks	0.296	0.988	1.186	1.58
Cisco	0.0035	0.019	0.044	0.02
Burbot				
Sticklebacks	0.87	2.84	3.5	4.68
Cisco	0.376	1.22	1.5	2.01
Pontoporeia	0.75	2.44	3.0	4.01
Coho (II)				
Sticklebacks	0.030	0.1	0.13	0.2
Coho (III)				
Sticklebacks	0.084	0.253	0.337	0.422
Cisco	0.0157	0.017	0.0627	0.0784

transport host to all predators were summed and added to the input to that transport host from *P. affinis*. The resultant proportional flow rates are shown on the arrows leading away from *P. affinis* in Figure 23.

The relative number of gravid *M. salmonis* from each host species was calculated as the abundance of *M. salmonis* times the proportion of gravid females in that host species (the second value in parentheses in Figure 23) times the weighting factor for the population of that host species. (The proportions of gravid females in whitefish and cisco were corrected for age and season using the procedures described above.) This value, divided by the sum of the values for all host species, was considered to be the relative output from that host species. These values are shown on the wide arrows leading to *P. affinis* in Figure 23. This calculation of output assumes that:

5. The turnover rate for gravid female *M. salmonis* is the same in all definitive host species;
6. The number of eggs per gravid female is the same in all definitive host species; and that
7. The probability of infecting *P. affinis* is the same for an egg from a gravid female from all definitive host species.

The model (Figure 23) shows that the majority of *M. salmonis* within the ecosystem flow through the basic life cycle from *P. affinis* to whitefish and back to *P. affinis*. A second major component is from *P. affinis* to cisco and back. Only about one-eighth of the flow was through transport hosts, primarily sticklebacks.

The output values in Figure 23 suggest that there are only three significant definitive hosts for *M. salmonis* in Cold Lake: whitefish, cisco and trout. Despite large populations of *M. salmonis* in individual coho, and a high proportion of gravid females, the relative abundance of coho is so low that acanthocephalans in this host account for only a small proportion of the [illegible] burbot and pike were relatively abundant (more so than [illegible] or coho), and both contain higher populations of *M. salmonis* [illegible] infected fish than cisco, but the low proportions of gravid females make the output from these host species negligible.

The population of *M. salmonis* in each of the three significant definitive hosts appeared to be controlled in different ways. In whitefish, the primary control appeared to be through a density-dependent regulation of the number of gravid females. There are three lines of evidence for this. First, the fairly constant mean number of gravid females in fish of age classes IV through IX, despite the tremendous increase in total numbers with age. Second, the fairly constant mean number of gravid females throughout the year, despite significant seasonal variation in total numbers. Third, and most instructive, the significant negative regression of percent gravid females on total numbers of acanthocephalans in individual fish. As a result of this control on maturation, the proportional output from whitefish was considerably less than the proportional input to whitefish. This type of negative feedback is an example of Bradley's (1972) Type III regulation (through the host individual), but operating on the output, rather than the "infra-population" (using the terminology of Esch *et al.*, 1975). This type of control is well-known in nematodes; for example, Michel (1970) showed that in equilibrium populations fifth-stage larvae of *Ostertagia ostertagi* could mature only when adults died.

In lake trout, the mean number of acanthocephalans and the mean number of gravid females were much higher than in whitefish, but the proportion of gravid females was much lower than in cisco or coho. The lake trout also harboured large numbers of *E. salvelini*. The multiple regression analysis showed the number of cestodes to be the most important variable determining the percent gravid females, explaining a substantial proportion (12%) of the variance (although, probably because of the small sample size, this proportion was not statistically significant). In this species of host, therefore, the regulation of maturation, and hence of output, appears to be a function of inter-specific interaction.

In contrast, there appeared to be no negative feedback system operating in cisco. Populations of *M. salmonis* in this host were low (mean of 8.7 per infected fish), but there was a high proportion (50%) of gravid females. Cisco appeared to acquire *M. salmonis* entirely through their relatively infrequent feeding on *P. affinis*. This appears to be an example of Bradley's (1972) Type I regulation (through transmission).

No negative feedback system appeared to be operating in coho, either, but in this host, populations of *M. salmonis* were very high, with a high proportion (57%) of gravid females. Perhaps this indicates that no regulation of population has been developed in this new host-parasite system.

The question arises: In which host does the regulation of the acanthocephalan population in the whole ecosystem take place? It might be in the intermediate host; I have no data on that part of the system. However, the model shows that most of the acanthocephalans in the ecosystem flow through whitefish. Using different mortality rates, this value varies between 2/3 and 3/4 of all acanthocephalans (Table 24). This high flow through the whitefish appears to be due to two factors, the abundance of whitefish in the lake, and the high proportion of *P. affinis* in their diet. The negative feedback operating through control of the rate of maturation of females reduces the output of eggs. This is the only significant, direct negative feedback I have found in the system, and appears to be the main regulator of the acanthocephalan population in the whole ecosystem.

Kennedy (1970, 1972) suggested that temperature and diet were important factors affecting recruitment of parasites, thus the population. He was unable to find any feedback mechanisms which regulated the population of *Pomphorhynchus laevis* in dace in the River Avon. However, the acanthocephalan showed little growth in dace (Hine and Kennedy, 1974b) and very few gravid female acanthocephalans (20/1864) were recovered from dace (Hine and Kennedy, 1974a). Perhaps, the *P. laevis*-dace system was not an appropriate system to study.

VIII. GENERAL DISCUSSION

I have shown that the patterns of infection by parasites and the resulting parasite communities in fish populations are influenced by host specificity, by seasonal factors and by the age and feeding habits of the fish hosts. In addition, the behaviour of the infective larvae and that of the host are also important. The interaction of these factors determined the pattern of species of parasites present and their abundances within the parasite community in each host species.

For parasite species which matured in more than one host species, these factors interacted in such a way that the parasite was generally much more abundant in one host species than in the others. This host species is regarded as the primary host (e.g., whitefish, for *M. salmonis*, as shown in Figure 24). Other host species in which this parasite matured, but in lesser abundance, are regarded as secondary hosts (e.g., cisco, trout, coho, pike, burbot, and walleye for *M. salmonis*).

The same type of analysis can be made for larval parasites (i.e., those for which the fish is a necessary intermediate host); that host species which harbours the greatest proportion of the larval stages is regarded as the primary host, others as secondary hosts.

The species of parasite assigned to different categories in each species of fish examined are shown in Table 26. In the primary and secondary host categories, larval parasites are in parentheses. Parasite species found in a host species, in a stage which could mature, but did not, are listed in the "Immature" category.

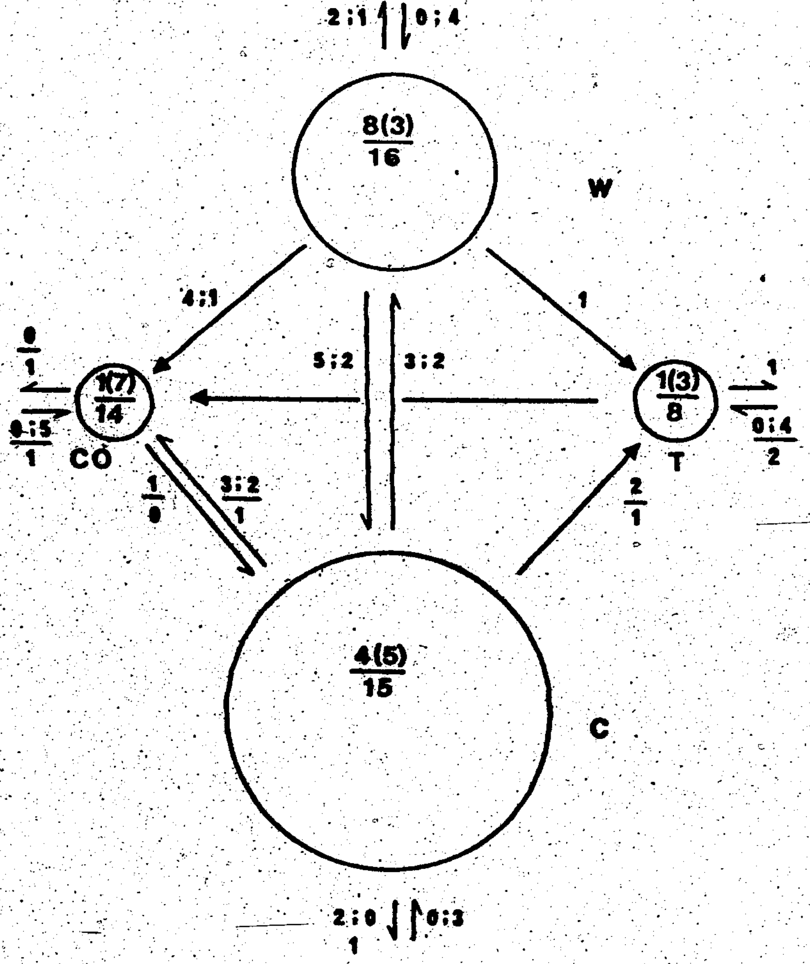
Whitefish are the primary hosts for the highest number of mature parasites (8), trout and coho for the least (1 each). Sticklebacks are

Figure 24. The number of species of parasites exchanged in a community of fishes in Cold Lake, Alberta. The exchanges within each of two subcommunities are shown separately. The sizes of the circles representing each host are proportional to the host population. Numbers within the circles are number of species mature in primary host (number of species mature in secondary host)/total number of species in that species of host. Arrows indicate exchange from a primary to a secondary host. Arrows leading to and from the periphery are exchanged with the other subcommunity. Values along arrows are the number of species which mature in the recipient host (number of species which do not mature)/number of species transferred from an intermediate or transport host to a definitive host. Where the number in parentheses in the numerator or the denominator is zero, it has been omitted. See text for detailed explanation.

Salmonid fishes: W - whitefish; C - cisco; T - lake trout; CO - coho salmon.

Non-salmonid fishes: P - pike; Ws - white sucker; Ln - longnose sucker; B - burbot; ST - ninespine sticklebacks; W - walleye.

SALMONID FISHES



NON-SALMONID FISHES

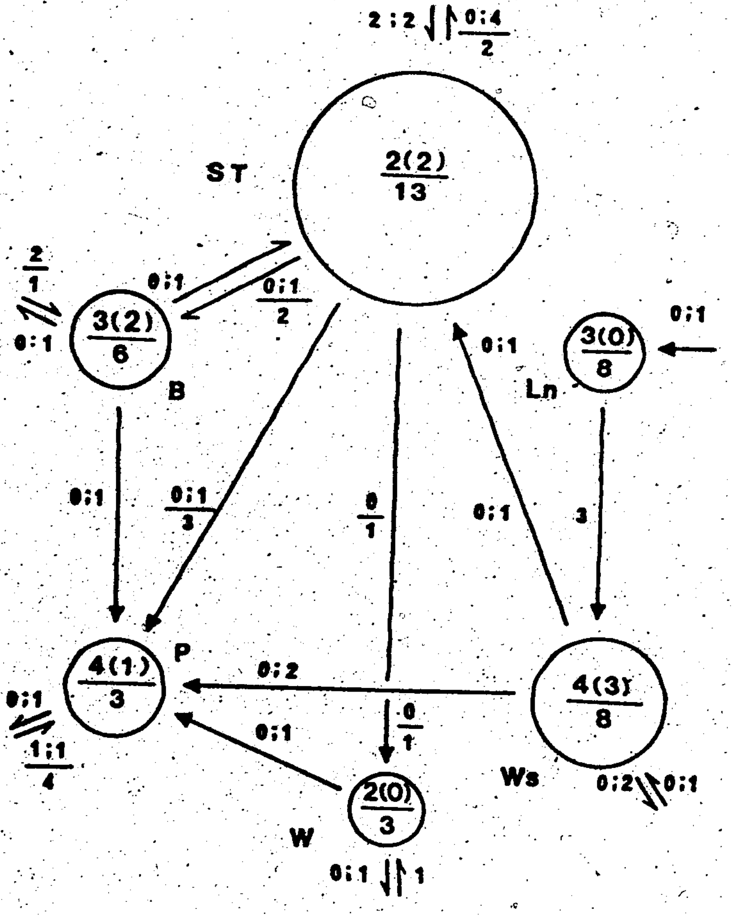


Table 26. Categorisation of the parasites in different species of fish in Cold lake, Alberta

	Primary	Secondary	Immature
Whitefish	*Discocotyle sagittata* *Phyllodistomum coregoni* *Cyathocephalus truncatus* *Proteocephalus exiguus* *Cystidicola stigmatura* *Metechinorhynchus salmonis* *Salmincola extensus* *Salmincola extumescens*	*Crepidostomum farionis* *Ergasilus auritus* *Ergasilus nerkae* *(Cotylurus erraticus)* *(Diplostomum spathaceum)* *(Diphyllobothrium* sp.*)*	*Pomphorhynchus bulbocolli* *Proteocephalus* spp.
Cisco	*Crepidostomum farionis* *Proteocephalus filicollis* *Ergasilus auritus* *Ergasilus nerkae* *(Diphyllobothrium* sp.*)* *(Triaenophorus crassus)*	*Discocotyle sagittata* *Cyathocephalus truncatus* *Philonema agubernaculum* *Metechinorhynchus salmonis* *Salmincola extensus* *(Cotylurus erraticus)*	*Cystidicola stigmatura* *Pomphorhynchus bulbocolli* *Proteocephalus* spp.
Trout	*Eubothrium salvelini*	*Metechinorhynchus salmonis* *Ergasilus auritus* *Ergasilus nerkae* *(Diplostomum spathaceum)* *(Triaenophorus nodulosus)* *(Raphidascaris* sp.*)*	*Pomphorhynchus bulbocolli*
Coho	*Philonema agubernaculum*	*Discocotyle sagittata* *Crepidostomum farionis* *Cyathocephalus truncatus* *Cystidicola stigmatura* *Metechinorhynchus salmonis* *Ergasilus auritus* *Ergasilus nerkae* *(Diphyllobothrium* sp.*)* *(Triaenophorus nodulosus)*	*Eubothrium* spp. *Neoechinorhynchus strigosum* *Pomphorhynchus bulbocolli* *Proteocephalus* spp.
Pike	*Proteocephalus pinguis* *Triaenophorus nodulosus* *Triaenophorus crassus* *Raphidascaris* sp.	*Metechinorhynchus salmonis* *(Schistocephalus solidus)*	*Neoechinorhynchus strigosum* *Proteocephalus* spp.
Whitesucker	*Lissorchis attenuatum* *Hunterella* sp. *Neoechinorhynchus strigosum* *Pomphorhynchus bulbocolli*	*Caryophyllaeus* sp. *Rhabdochona cascadilla* *Ergasilus* sp.	*Metechinorhynchus salmonis*
Longnose sucker	*Caryophyllaeus* sp. *Rhabdochona cascadilla* *Ergasilus* sp.		*Metechinorhynchus salmonis*
Burbot	*Eubothrium rugosum* *Haplonema* sp. *Cystobranchus verrilli*	*Cyathocephalus truncatus* *Metechinorhynchus salmonis* *(Triaenophorus nodulosus)*	
Stickleback	*Bunodera luciopercae* *Gyrodactylus* sp. *(Cotylurus erraticus)* *(Diplostomum spathaceum)* *(Apatemon gracilis)* *(Schistocephalus solidus)* *(Triaenophorus nodulosus)* *(Raphidascaris* sp.*)*	*Proteocephalus filicollis* *Ergasilus auritus*	*Pomphorhynchus bulbocolli* *Eubothrium* spp. *Metechinorhynchus salmonis*
Walleye	*Proteocephalus* sp. *Bothriocephalus cuspidatus*		*Metechinorhynchus salmonis*

the primary hosts for the most species of larval parasites (6). Coho acted as a secondary host to the largest number of species of parasites (9).

It is apparent that there is a fair amount of exchange of parasites within the community of fishes. This exchange of species of parasites among host species is illustrated in Figure 24, in which the salmonid and non-salmonid portions of the community are shown separately. The size of the circles represents the proportion of the host species within the community of fishes, as given in Table 26. The values within each circle are:

number of species mature, in primary host
(number of species mature, in secondary host)
total number of species in that host

The arrows between species in each portion of the community indicate the direction of exchange of parasites, from primary to secondary or "immature" hosts. Values along each arrow are:

number of species which mature in recipient;
number which do not mature in recipient
number of species transferred from intermediate or transport host to a definitive host.

The short arrows peripheral to the circles indicate transfer to or from the other portion of the community.

The Figure shows that there is a considerable amount of exchange of parasites within the salmonids, especially between the two most abundant native species, whitefish and cisco. These two species exchange 11 out of the 14 species (12 of which mature in one or both) for which one is the primary host. Trout appear to be somewhat isolated from this exchange; they are the primary host for only a single species, which is not shared with the other native salmonids, and acquire only three (including *M. salmonis*) of the 14 species for which the native salmonids are the primary host.

The introduced coho are the primary host for only one species, *P. agubernaculum*, which is shared only with cisco. However, coho acquired almost all of the parasites for which the other salmonids are the primary host; seven of the eleven parasites matured in coho. In total, there are 16 species for which salmonids are the primary host; 13 of these are shared by two or more of the salmonids.

Another measure of the extent of the exchange between salmonids is the number of species shared per pair of host species. This number ranged from one to eleven, with a mean of 4.3. In contrast, the same measure applied to the exchange between non-salmonid fishes ranged from zero to three, with a mean of 0.7. Of the 24 species of parasites for which non-salmonids are the primary hosts, only 12 are shared by two or more species of non-salmonid fishes. These two features indicate the restricted exchange of parasites between non-salmonid fishes.

The greatest exchange, and the only one in which the parasites mature in both species, is between the two cyprinids. In this case, white suckers acquire all three parasites for which longnose suckers are the primary host, but longnose suckers do not acquire any of the four species for which white suckers are the primary host. At present, no reason for this is apparent.

The exchanges of parasites between the two groups of fishes are quite different. The transfer of parasites of salmonids to non-salmonids involves five of the 16 species, and includes four which mature in the non-salmonids. (However, see the discussion on *M. salmonis* (p. 128) for an alternative interpretation for that species.) Two of these are spread from cisco to sticklebacks, thus involving the two most abundant species of fish in the lake. On the other hand, the transfer of parasites from non-salmonids to salmonids involves six of the 24 species, but none mature in the salmonids. Most are larval forms, largely species for which sticklebacks are the primary intermediate host.

In addition to these exchanges of parasites, in which the fish hosts harbour the same stage of the parasite, there are also "life cycle transfers," in which the parasites flow from intermediate or transport hosts to the definitive host. These transfers, shown as the denominators on the arrows in Figure 24, occur at approximately equal frequencies within the two groups, with rather extensive transfers between groups. The latter appears to be due to extensive feeding on sticklebacks by trout and coho, and on cisco by pike and burbot.

Special attention should be paid to the introduced coho. All eight species which matured in the coho are shared with other salmonids; included are three of the four species from salmonids which also matured in non-salmonids. One of these is the ubiquitous *M. salmonis*. Two of the remaining species are larvae, of *Diphyllobothrium* sp. (for which cisco are the primary hosts) and *T. nodulosus* (for which sticklebacks are the primary hosts). The other four species were always immature; they include two species of acanthocephalans for which suckers are the primary hosts, and plerocercoids of *Eubothrium* and *Proteocephalus* which could not be identified to species. These could have been acquired from salmonid or non-salmonid fishes. In general, then, the important parasites of coho were derived from the dominant native salmonid fishes.

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Appendix I. Indices of dominance of the parasites in each species of fish in Cold Lake, Albérta, and in the entire community of fishes

	Community		Whitefish	Cisco	Trout	Coho	Pike	White sucker	Longnose sucker	Burbot	Stickleback	Walleye
	Unwtd	Wtd										
Metechinorhynchus salmonis	75.2	52.3	79.6	9.8	91.3	91.1	19.1			92.7		
Proteocephalus spp.*	4.5	15.4	1.1	50.3		0.2	44.9					
Cyathocephalus truncatus	1.7	6.1	9.7	0.9		0.004				0.1		
Ergasilus nerkae	1.3	4.9	0.3	16.1	0.006	6.1						
Ergasilus auritus	0.9	3.3	0.1	10.4	1.5	0.6					2.2	
Gyrodactylus sp.	0.4	2.9									37.2	
Proteocephalus filicollis	0.2	2.8		9.3							1.6	
*Cotylurus erraticus***	0.5	2.8	1.8	0.08							21.3	
Cystidicola stigmatura	0.8	2.8	4.6			0.07						
Diplostomum spathaceum	0.3	2.1	0.007		0.001						26.7	
Discocotyle sagittata	0.3	1.2	1.3	1.5		0.002						
Pomphorhynchus bulbocolli	3.0	0.8						95.9				
Proteocephalus exiguus	0.1	0.5	0.9									
Metechinorhynchus salmonis (cystacanth)	2.2	0.4						80.8	69.9		1.9	14.3
Diphyllobothrium sp.**	0.03	0.3	0.0005	0.1		0.04						
*Schistocephalus solidus***	0.03	0.3					0.04				2.7	
Triaenophorus nodulosus	2.5	0.2					35.4					
Salmincola extensus	0.05	0.2	0.3	0.003								
Salmincola extumescens	0.03	0.1	0.2									
*Triaenophorus nodulosus***	0.04	0.1			0.01	0.02				0.1	1.3	
*Apatemon gracilis***	0.02	0.2									2.4	
Bunodera luciopercae	0.01	0.1									0.9	
Rhabdochona cascadilla	0.5	0.1						0.3	16.3			
*Pomphorhynchus bulbocolli**	0.02	0.1	0.009	0.2	0.001	0.06					0.07	
Eubothrium rugosum	0.8	0.1								5.4		
Philonema agubernaculum	0.2	0.1		0.2		1.7						
Eubothrium salvelini	2.6	0.1			7.1							
Caryophyllaeus sp.	0.3	0.04						0.4	10.5			
*Cystidicola stigmatura**	0.003	0.04		0.1								
Eubothrium spp.*	0.01	0.03				0.04					0.4	
Crepidostomum farionis	0.01	0.03	0.0009	0.09		0.09						
Bothriocephalus cuspidatus	0.6	0.02										52.9
Ergasilus sp.	0.1	0.02						0.7	3.3			
Haplonema sp.	0.2	0.02								1.5		
Phyllodistomum coregoni	0.004	0.02	0.03									
Proteocephalus sp.* (A)	0.4	0.01										32.8
*Triaenophorus crassus***	0.0007	0.008			0.03							
Lissorchis attenuatum	0.03	0.007						0.8				
Neoechinorhynchus strigosum	0.03	0.007						0.8				
Proteocephalus pinguis	0.03	0.002					0.4					
Hunterella sp.	0.007	0.002						0.2				
Raphidascaris sp.*	0.01	0.001			0.03						0.02	
Cystobranchus verrilli	0.02	0.001								0.1		
*Neoechinorhynchus strigosum**	0.007	0.0004				0.01	0.07					
Triaenophorus crassus	0.004	0.0003					0.05					
Raphidascaris sp.	0.004	0.0003					0.05					

*Immature.

**Larval.

Appendix 11. Comparison of the parasite communities in different age classes of lake whitefish

AGE PARASITES	II	III	IV	V	VI	VII	VIII	IX	X
Discocotyle sagittata	24.3 (2.4)[A]	80.6 (3.6)	74.4 (5.7)	75.6 (5.9)	73.1 (4.4)	60.8 (3.6)	70.4 (3.0)	62.8 (3.6)	89.5 (2.6)
Crepidostomum farionis	0	0	0	1.2 (1.0)	0	0.4 (1.0)	0.8 (1.0)	0	0
***Cotylurus erraticus*	8.1[C]	33.3	47.4	53.6	41.9	43.9	51.3	53.1	68.4
***Diplostomum spathaceum*	0	0	1.3 (1)	1.2 (1)	3.2 (1)	0	2.1 (1)	0.8 (1)	0
Phyllodistomum coregoni	0	0	6.4 (4.2)	2.4 (1.5)	4.3 (3.0)	0.7 (1.0)	1.3 (2.3)	0.8 (1.0)	5.3 (2)
Proteocephalus exiguus	13.5 (9.6)	38.9 (18.3)	32.1 (9.3)	29.3 (18.7)	16.1 (11.6)	6.1 (10.3)	6.3 (8.5)	8.5 (7.1)	10.5 (2)
**Proteocephalus* spp.	10.8 (11.5)	16.7 (9.3)	21.8 (10.5)	25.6 (24.1)	16.1 (21.1)	14.2 (4.6)	17.5 (8.7)	16.2 (4.9)	15.8 (6)
Cyathocephalus truncatus	24.3 (3.1)	55.6 (7.5)	69.2 (12.0)	72.0 (25.5)	73.1 (18.9)	75.6 (26.8)	78.3 (18.4)	80.8 (40.6)	84.2 (20.9)
***Diphyllobothrium* sp.	0	0	0	0	0	0	0.4 (1.0)	1.5 (1.0)	0
Cystidicola stigmatura	43.2 (9.0)	83.3 (8.9)	79.5 (8.5)	74.4 (9.9)	73.1 (9.7)	72.3 (13.4)	79.6 (15.2)	79.2 (13.4)	89.5 (13.1)
Metechinorhynchus salmonis	83.8 (7.1)	100 (43.5)	98.7 (68.2)	100 (113.5)	100 (126.5)	100 (189.4)	100 (205.1)	100 (265.3)	100 (241.5)
**Pomphorhynchus bulbocolli*	5.4 (3.5)	0	0	0	1.1 (1.0)	1.4 (2.0)	0.4 (5.0)	0	0
Ergasilus nerkae	40.5 (15.7)	5.6 (13.0)	6.4 (2.6)	4.9 (38.0)	4.3 (3.5)	3.4 (9.2)	2.1 (4.8)	0.8 (17.0)	5.3 (3.0)
Ergasilus auritus	10.8 (10.8)	5.6 (11.5)	0	0	0	0.7 (3.0)	0.8 (67.0)	0.8 (17.0)	0
Salmincola extensus	5.4 (1.0)	30.6 (1.4)	52.6 (1.8)	45.1 (1.7)	39.8 (1.9)	25.0 (1.8)	24.5 (1.9)	20.8 (1.6)	5.3 (1)
Salmincola extumescens	2.7 (1.0)	8.3 (1.3)	7.7 (1.2)	8.5 (1.0)	8.6 (1.0)	24.3 (1.6)	40.8 (1.6)	54.6 (1.8)	57.9 (1.3)
n***	37	36	78	82	93	148	240	130	19
I	37	36	28	82	93	148	240	130	19
FL (cm)	17.1	24.8	30.0	32.4	37.5	39.3	41.3	42.6	43.0
S	12	11	12	13	14	13	16	15	11
$\bar{S}$	2.73[B] (±0.22)	4.67 (±0.28)	5.13 (±0.16)	5.15 (±0.15)	4.75 (±0.15)	4.47 (±0.10)	4.73 (±0.078)	5.05 (±0.12)	5.32 (±0.30)
$\bar{N}$	22.19 (±3.47)	71.11 (±10.37)	97.17 (±6.88)	160.45 (±13.46)	159.34 (±12.86)	209.28 (±9.87)	241.36 (±11.71)	318.32 (±23.97)	318.47 (±46.76)
SI	5.06	2.50	2.01	1.97	1.58	1.42	1.38	1.41	1.34
H'	1.88	1.40	1.19	1.15	0.87	0.68	0.66	0.65	0.60
E	0.75	0.58	0.48	0.45	0.33	0.26	0.24	0.25	0.25

* Larval

** Immature

*** The abbreviations are denoted as follow: No. examined (n); No. infected (I); Fork length of fish (FL); No. spp. parasites (S); Mean No. spp. parasites ($\bar{S}$); Mean No. individual ($\bar{N}$); Simpson's Index (SI); Shannon-Weaver Index (H'); Evenness (E).

A. Prevalence (mean intensity)
B. Mean (± S. E.)
C. Prevalence only.

Appendix III. Comparison of the parasite communities in different age classes of cisco

AGE PARASITES	I	II	III	IV	V
Discocotyle sagittata	10.9 (1.0)^{A}	25.4 (2.2)	14.6 (2.0)	18.8 (2.0)	25.6 (2.6)
***Cotylurus erraticus*	0^{C}	0	0	1.8	1.0
Crepidostomum farionis	2.2 (2.0)	9.5 (2.0)	4.9 (3.3)	1.8 (2.6)	1.5 (1.0)
Cyathocephalus truncatus	0	0	3.0 (1.0)	9.9 (2.6)	12.1 (18.5)
Proteocephalus filicollis	8.7 (14.3)	23.8 (9.4)	26.1 (9.6)	19.1 (14.6)	18.6 (9.8)
**Proteocephalus* spp.	54.4 (8.1)	63.5 (26.3)	69.7 (35.0)	51.8 (29.6)	41.7 (16.8)
***Diphyllobothrium* sp.	17.4 (1.3)	15.9 (1.3)	17.0 (1.3)	13.5 (1.4)	16.6 (2.5)
***Triaenophorus crassus*	0	0	0	1.1 (1.3)	1.0 (1.0)
**Cystidicola stigmatura*	0	0	0.6 (1.0)	1.4 (4.8)	1.0 (1.0)
Philonema agubernaculum	0	0	0	0.6 (4.0)	2.0 (4.3)
Metechinorhynchus salmonis	10.9 (5.0)	28.6 (8.2)	26.1 (10.6)	34.8 (8.1)	38.2 (8.8)
**Pomphorhynchus bulbocolli*	0	4.8 (1.7)	1.8 (2.0)	1.1 (4.7)	0
Ergasilus auritus	30.4 (7.1)	34.9 (10.9)	34.6 (13.8)	21.6 (13.3)	18.6 (10.2)
Ergasilus nerkae	17.4 (36.1)	46.0 (24.7)	29.7 (17.7)	31.9 (8.2)	40.2 (12.5)
Salmincola extensus	0	0	0	0.4 (1.0)	0
n***	46	63	165	282	199
I	36	55	158	249	174
S	8	9	12	15	13
$\bar{S}$	2^{B} (±0.21)	2.89 (±0.16)	2.41 (±0.10)	2.38 (±0.08)	2.54 (±0.11)
$\bar{N}$	19.43^{B} (±4.61)	42.95 (±6.61)	43.30 (±6.61)	31.45 (±4.48)	25.84 (±3.25)
SI	3.45	3.24	2.49	2.84	3.19
H'	1.45	1.43	1.29	1.45	1.84
E	0.69	0.65	0.51	0.53	0.71

See Appendix II for abbreviations and format.

Appendix IV. Seasonal variation in the parasite communities in group A lake whitefish (age classes IV and V)

MONTHS PARASITES	J	F	M	A	M	J	J	A	S	O	N	D
Discocotyle sagittata	76 (6)^A	50 (3)	83.3 (5.2)	75 (1)	56.3 (4.7)	85 (5.1)	73.1 (5.8)	100 (6.9)	66.7 (6.3)	66.7 (5)	83.3 (5)	61.9 (7.5)
***Cotylurus erraticus*	75^C	100	66.7	25	56.3	35	34.6	37.5	66.7	0	100	61.9
Cyathocephalus truncatus	75 ([illegible].7)	100 (29.5)	100 (6.5)	50 (1.5)	81.3 (7.8)	75 (11.9)	65.4 (12.6)	37.5 (2.3)	66.7 (25)	66.7 (9)	83.3 (10.8)	95.2 (33.9)
Phyllodistomum coregoni	0	0	0	0	23.1 (3)	0	3.9 (1)	0	0	0	0	0
Proteocephalus exiguus	0	0	16.7 (1)	0	23.1 (59)	25 (32)	57.7 (11.9)	37.5 (6.7)	50 (6.7)	33.3 (8)	16.7 (1)	0
**Proteocephalus* spp.	62.5 (38.4)	50 (2)	50 (8)	25 (1)	31.3 (37.6)	30 (10)	11.5 (12)	0	16.7 (1)	0	33.3 (34)	42.9 (11.6)
Cystidicola stigmatura	100 (11.6)	100 (19)	100 (23.2)	75 (10.3)	93.8 (10.2)	90 (10.7)	69.2 (4.9)	37.5 (4.3)	66.7 (3.3)	66.7 (4)	83.3 (8.6)	90.5 (10.1)
Metechinorhynchus salmonis	75 (171.7)	100 (98.5)	100 (87.3)	100 (71.3)	93.8 (88.1)	100 (71.2)	100 (101.8)	100 (103.6)	83.3 (96.6)	100 (57.3)	100 (93)	100 (138.4)
Ergasilus nerkae	0	0	0	0	0	10 (1.5)	0	0	0	0	0	0
Salmincola extensus	25 (3)	0	50 (1.7)	50 (1)	56.3 (1.7)	50 (2.4)	61.5 (1.3)	50 (1.3)	33.3 (1.5)	66.7 (1.5)	66.7 (2)	47.6 (1.8)
Salmincola extumescens	0	0	16.7 (1)	25 (1)	0	0	3.9 (1)	25 (1)	0	0	0	0
n***	8	2	6	4	16	20	26	8	6	3	6	21
I	8	2	6	4	16	20	26	8	6	3	6	21
S	7	6	9	8	9	9	10	8	8	6	8	7
$\bar{S}$	5.38^B (±0.38)	5.0 (±1.0)	5.83 (±0.40)	4.50 (±0.29)	5.19 (±0.31)	5.0 (±0.23)	4.77 (±0.28)	4.50 (±0.63)	4.67 (±1.02)	4.33 (±1.2)	5.67 (±0.42)	5.0 (±0.25)
$\bar{N}$	224.58 (±40.3)	155.5 (±80.5)	130.83 (±40.47)	87.25 (±29.05)	129.94 (±22.94)	108.3 (±15.39)	128.92 (±21.01)	119.88 (±18.61)	117.83 (±44.37)	75 (±50.85)	128.83 (±33.60)	193.95 (±35.48)
SI	2.52	2.18	2.04	1.33	2.26	2.19	1.58	1.30	1.81	1.59	1.87	1.84
H'	1.21	1.05	1.09	0.56	1.27	1.24	0.88	0.57	0.96	0.84	1.05	0.96
E	0.62	0.58	0.49	0.27	0.58	0.56	0.38	0.27	0.46	0.47	0.51	0.49

See Appendix II for abbreviations and format

Appendix V. Seasonal variations in the parasite communities in group B lake whitefish (age classes VII and VIII)

MONTHS PARASITES	J	F	M	A	M	J	J	A	S	O	N	D
Discocotyle sagittata	61.5 (3.6)^{A}	73.3 (2.3)	57.1 (3.3)	61.9 (3.2)	73.9 (2.1)	60 (3.7)	67.9 (3.1)	73.3 (3.2)	73.1 (3.8)	76.2 (2.5)	74.2 (3.9)	50 (3.5)
***Cotylurus erraticus*	69.2^{C}	60	40.5	71.4	85.2	51.1	56.6	42.2	26.9	28.6	51.6	41.7
Cyathocephalus truncatus	92.3 (42.8)	73.3 (52.2)	85.7 (18.3)	61.9 (4.2)	95.7 (22)	84.4 (41.5)	69.8 (53.1)	60 (24.5)	46.2 (15.2)	76.2 (16.5)	87.1 (26.[illegible])	91.7 (46.8)
***Diphyllobothrium* sp.	0	0	0	0	0	0	0	0	0	4.8 (1)	0	0
***Diplostomum spathaceum*	0	0	0	0	0	0	9.4 (1)	0	0	0	0	0
Phyllodistomum coregoni	7.7 (1)	0	0	9.5 (1)	4.3 (1)	0	1.9 (5)	0	0	0	0	0
Proteocephalus exiguus	0	0	7.1 (14.3)	0	13 (7.7)	8.9 (11.8)	22.6 (5.8)	2.2 (2)	0	0	0	0
**Proteocephalus* spp.	76.9 (37.7)	33.3 (5)	21.4 (23.8)	33.3 (2.6)	21.7 (3.8)	26.7 (3.9)	5.7 (4)	0	0	4.8 (1)	3.2 (15)	19.4 (5.7)
Cystidicola stigmatura	92.3 (28.5)	100 (16.4)	85.7 (25.9)	100 (19.1)	78.3 (11.3)	80 (12.2)	54.7 (5.2)	55.6 (3.6)	61.5 (2.8)	76.2 (7.4)	87.1 (14.9)	88.9 (18)
Metechinorhynchus salmonis	100 (218.5)	100 (174.2)	100 (146.6)	100 (88.8)	100 (189.8)	100 (226)	100 (269.9)	100 (163.4)	100 (102.8)	100 (144.4)	100 (254.7)	100 (258.3)
**Pomphorhynchus bulbocolli*	0	0	2.4 (3)	0	0	0	0	0	3.8 (1)	0	0	0
Ergasilus auritus	0	13.3 (12)	0	0	0	0	0	0	0	0	0	2.8 (113)
Ergasilus nerkae	0	0	0	0	0	0	0	22.2 (7)	0	0	0	0
Salmincola extensus	53.8 (1.3)	13.3 (2)	42.9 (1.8)	33.3(1.1)	34.8 (1.5)	28.9 (1.5)	24.5 (1.9)	28.9 (2.1)	19.2 (1.2)	23.8 (1.8)	38.7 (3.4)	13.9 (1.2)
Salmincola extumescens	23.1 (2.3)	40 (1.3)	21.4 (1.6)	47.6 (1.9)	47.8 (2.2)	48.9 (1.9)	22.6 (1.3)	37.8 (1.7)	34.6 (1.8)	9.6 (1.3)	25.9 (1.1)	27.8 (1.3)
n	13	15	42	21	23	45	53	45	26	21	31	36
I	13	15	42	21	23	45	53	45	26	21	31	36
S	9	9	10	9	10	9	11	9	8	9	8	9
$\bar{X}$	5.85 (±0.30)	5.21 (±0.26)	4.60 (±0.21)	5.24 (±0.3)	5.35 (±0.24)	4.93 (±0.18)	4.40 (±0.16)	4.00 (±0.16)	3.65 (±0.22)	4.05 (±0.26)	4.68 (±0.21)	4.48 (±0.22)
$\bar{N}$	322.31 (±40.14)	256.6 (±39.72)	196.93 (±16.0)	120.43 (±12.99)	229.91 (±31.60)	274.46 (±21.86)	318.92 (±30.05)	188.69 (±20.93)	117.46 (±20.24)	168.0 (±26.88)	299.74 (±30.29)	336.4 (±33.08)
SI	2.04	1.78	1.73	1.75	1.45	1.50	1.37	1.32	1.38	1.33	1.37	1.55
H'	1.07	0.91	0.93	0.91	0.71	0.72	0.58	0.58	0.55	0.57	0.61	0.75
E	0.49	0.41	0.40	0.41	0.31	0.33	0.24	0.26	0.26	0.26	0.29	0.34

See Appendix II for abbreviations and format

Appendix VI. Seasonal variations in the parasites communities in cisco (age classes IV and V)

PARASITES / MONTHS	J	F	M	A	M	J	J	A	S	O	N	D
Discocotyle sagittata	34.5 (1.9)[A]	41.3 (2)	17.5 (1.6)	29.4 (1.6)	20.6 (4.3)	8.7 (2.7)	11.3 (1.4)	10.4 (2.1)	37.5 (2)	53.6 (2.4)	29 (2.4)	22.9 (2.8)
***Cotylur[illegible]aticus*	3.4[B]	0	0	2.9	8.8	0	0	1.5	0	0	3.2	0
Crepidostomum farionis	0	0	0	0	0	0	0	0	0	3.6 (1)	0	0
Cyathocephalus truncatus	0	23.5 (11.5)	10 (6.3)	2.9 (9)	14.7 (12.2)	4.3 (1.7)	6.5 (3.5)	11.9 (2.3)	5 (1)	25 (4)	9.7 (1.7)	17.1 (3)
***Diphyllobothrium* sp.	13.8 (2.3)	0	30 (2.3)	38.2 (1.8)	23.5 (3.3)	15.9 (1.5)	6.5 (1.3)	11.9 (1.5)	75 (1.7)	14.3 (1.5)	9.7 (1)	8.6 (1.3)
Proteocephalus filicollis	17.2 (7.4)	0	5 (7)	0	23.5 (11.1)	7.2 (17.8)	19.4 (8.4)	52.2 (17.5)	47.5 (10.6)	10.7 (1)	54.8 (7.2)	5.7 (2.5)
**Proteocephalus* spp.	13.8 (3.8)	0	65 (22.5)	44.1 (151.3)	32.4 (29.6)	46.4 (19.4)	50 (17.6)	52.2 (10.3)	67.5 (8.8)	14.3 (12.8)	9.7 (1)	77.1 (20.9)
***Triaenophorus crassus*	0	0	0	0	0	1.4 (1)	0	1.5 (1)	2.5 (2)	0	6.5 (1)	0
**Cystidicola stigmatura*	0	0	5 (3.5)	5.9 (1)	11.8 (1.5)	0	1.6 (1)	0	0	0	0	0
Philonema agubernaculum	6.9 (3.5)	0	0	2.9 (5)	0	0	3.2 (5)	0	0	0	0	0
Metechinorhynchus salmonis	37.9 (4.8)	41.3 (7.1)	32.5 (8)	26.5 (11.1)	38.2 (6.5)	42 (4.3)	33.9 (7.9)	34.3 (7.8)	37.5 (7.9)	50 (20.1)	35.5 (8.2)	40 (12.4)
**Pomphorhynchus bulbocolli*	0	0	0	0	0	0	1.6 (1)	3 (4.5)	0	3.6 (5)	0	0
Ergasilus auritus	17.2 (3.2)	35.3 (2.3)	40 (5.1)	35.3 (25.7)	35.3 (19.1)	13 (18.9)	14.5 (4.7)	9.0 (7.8)	22.5 (12.6)	32.1 (16)	9.7 (1.7)	5.7 (4.5)
Ergasilus nerkae	27.6 (4)	35.3 (1.5)	35 (3.6)	26.5 (1.9)	17.6 (4.2)	8.7 (10.7)	19.4 (44.4)	50.7 (7.6)	80 (23.5)	78.6 (11.7)	22.6 (5.6)	45.7 (4.6)
Salmincola extensus	0	0	0	0	0	0	0	0	0	3.6 (1)	0	0
n***	29	17	40	34	34	69	62	67	40	28	31	35
I	23	15	36	27	28	56	50	57	40	25	30	34
S	9	5	9	10	10	10	12	11	10	10	10	8
$\bar{S}$	2.26[C] (±0.23)	2.00 (±0.24)	2.64 (±0.26)	2.70 (±0.37)	2.73 (±0.25)	1.91 (±0.14)	2.12 (±0.18)	2.70 (±0.18)	3.05 (±0.22)	3.24 (±0.29)	2.00 (±0.21)	2.29 (±0.20)
$\bar{N}$	8.70 (±2.16)	8.87 (±4.08)	24.75 (±5.86)	101.74 (±35.64)	31.43 (±7.61)	20.02 (±4.04)	19.65 (±2.70)	24.47 (±3.12)	37.45 (±11.55)	32.58 (±5.64)	9.87 (±2.23)	25.91 (±3.96)
SI	6.03	3.48	2.24	1.44	4.41	2.78	3.3	3.79	3.09	3.87	3.49	2.13
H'	1.96	1.39	1.27	0.67	1.77	1.40	1.44	1.56	1.43	1.56	1.52	1.09
E	0.89	0.86	0.57	0.29	0.77	0.60	0.57	0.64	0.62	0.67	0.65	0.52

See Appendix II for abbreviations and format

Appendix VII. Comparison of the food of different age classes of lake whitefish

Food Items \ Age	II	III	IV	V	VI	VII	VIII	IX
Stickleback	0*	0	0	2.0	6.1	0	1.3	3.5
Nematomorpha	0	0	0	0	6.1	0	0	0
Glossiphoniidae	12.1	18.8	13.6	7.8	9.1	8.5	13.2	5.2
Mysis relicta	0	0	0	0	0	0	1.3	0
Pontoporeia affinis	51.5	37.5	68.2	60.8	60.6	74.5	77.6	89.7
Hyallela asteca	12.1	18.8	9.1	9.8	12.1	4.3	14.5	10.3
Gammarus lacustris	3.0	43.8	11.4	23.5	15.2	21.3	25.0	12.1
Ephemeroptera	9.1	0	4.6	0	0	6.4	0	1.7
Corixidae	0	0	0	0	0	6.4	0	0
Trichoptera	0	12.5	6.8	7.8	3.0	19.1	21.1	15.5
Tendipedidae	48.5	68.8	63.6	37.3	42.4	46.8	56.6	53.5
Physidae	0	0	9.1	7.8	3.0	8.5	1.3	3.5
Planorbidae	0	0	0	0	0	0	0	1.7
Sphaeriidae	42.4	56.3	65.9	52.9	63.6	66.0	68.4	72.4
Fish egg	0	0	11.4	21.6	15.2	17.0	6.6	6.9
Vegetation	0	0	4.6	2.0	15.2	6.4	4.0	1.7
n**	41	25	59	62	43	53	119	86
IF	33	16	44	51	33	47	76	58
SF	7	6	11	11	12	12	12	13
$\overline{SF}$ (±S.E.)	1.85*** (±0.12)	2.63 (±0.18)	2.75 (±0.16)	2.33 (±0.15)	2.64 (±0.20)	2.81 (±0.71)	2.93 (±0.14)	2.84 (±0.16)
SI	4.44	4.99	5.41	5.88	6.15	6.03	5.48	4.65
H'	1.64	1.69	1.94	1.98	2.09	2.06	1.92	1.85
E	0.82	0.94	0.77	0.80	0.79	0.81	0.75	0.66

*Prevalence - percentage, out of stomach with some food.

**The abbreviations are denoted as follow: No. examined (n); No. with food (IF); No. food items (SF); Mean no. food items ($\overline{SF}$); Simpson's index (SI); Shannon-Weaver index (H'); Evenness (E).

***Mean (±S.E.).

Appendix VIII. Seasonal variations in the food of group A lake whitefish (age classes IV and V)

Food Items \ Months	J	F	M	A	M	J	J	A	S	O	N	D
Stickleback	0*	0	0	0	0	0	0	0	0	0	16.7	0
Glossiphoniidae	0	0	0	0	16.7	0	21.1	28.6	50	0	0	0
Mysis relicta	0	50	0	25	0	0	0	0	0	0	0	0
Pontoporeia affinis	75	100	0	25	66.7	100	68.4	71.4	75	0	50	35
Hyallela azteca	0	0	0	0	25	0	0	28.6	0	33.3	16.7	5
Gammarus lacustris	12.5	0	0	0	8.3	0	10.5	42.9	0	100	33.3	45
Ephemeroptera	0	0	0	0	25	0	0	0	0	0	0	0
Trichoptera	12.5	0	0	0	16.7	0	5.3	0	0	0	0	15
Tendipedidae	12.5	50	0	25	66.7	92.9	68.4	57.1	75	0	16.7	10
Physidae	0	0	0	0	8.3	0	15.8	28.6	25	33.3	0	0
Sphaeriidae	12.5	50	0	25	83.3	78.6	89.5	42.9	75	33.3	66.7	20
Fish Eggs	12.5	0	0	0	0	0	0	0	0	0	0	80
Vegetation	0	0	0	0	0	0	10.5	0	0	0	0	0
[illegible]	9	2	6	4	16	16	25	8	6	3	6	21
IF	8	2	0	1	12	14	19	7	4	3	6	20
SF	6	4	0	4	9	3	8	7	5	4	6	7
$\overline{SF}$	1.38***	2.5	0	4.0	3.17	2.71	2.89	3.0	3.0	2.0	2.0	2.1
(±S.E.)	(±0.26)	(±1.5)			(±0.37)	(±0.16)	(±0.21)	(±0.44)	(±0.71)		(±0.37)	(±0.19)
SI	2.95	3.57	0	4	5.64	3.0	4.58	6.21	4.5	3.0	4.5	4.24
H'	1.42	1.33	0	1.39	1.91	1.10	1.71	1.89	1.55	1.24	1.63	1.64
E	0.76	0.96	0	1.0	0.86	1.0	0.81	0.97	0.96	0.89	0.90	0.83

*Prevalence - percentage, out of stomach with some food.

**The abbreviations are denoted as follow: No. examined (n); No. with food (IF); No. food items (SF); Mean no. food items ($\overline{SF}$); Simpson's index (SI); Shannon-Weaver index (H'); Evenness (E).

***Mean (±S.E.).

Appendix IX. Seasonal variation in food of group B lake whitefish (age classes VII and VIII)

Months / Food Items	J	F	M	A	M	J	J	A	S	O	N	D
Stickleback	0*	0	11.1	0	0	0	0	0	0	0	0	0
Glossiphoniidae	0	0	0	0	23.5	27.8	8.3	0	0	36.4	0	0
Mysis relicta	16.7	0	0	0	0	0	0	0	0	0	0	0
Pontoporeia affinis	50	66.7	11.1	87.5	76.5	100	100	83.3	100	63.6	92.3	66.7
Hyallela asteca	0	0	66.7	12.5	23.5	5.6	8.3	0	0	0	0	0
Gammarus lacustris	33.3	0	66.7	25	41.2	5.6	8.3	0	0	27.3	7.7	27.8
Ephemeroptera	0	0	0	0	5.9	5.6	0	0	0	0	0	0
Corixidae	0	0	0	0	0	5.6	0	0	0	9.1	0	0
Trichoptera	33.3	33.3	11.1	75	35.3	11.1	0	0	0	9.1	15.4	27.8
Tendipedidae	33.3	33.3	33.3	25	76.5	77.8	83.3	66.7	50	9.1	53.8	44.4
Physidae	0	0	11.1	0	5.9	5.6	0	0	0	9.1	0	5.6
Sphaeriidae	50	33.3	44.4	50	76.5	83.3	66.7	83.3	50	90.9	84.6	50
Fish Eggs	16.7	33.3	0	0	0	0	0	0	0	0	0	72.2
Vegetation	0	0	22.2	0	0	5.6	8.3	0	0	9.1	0	5.6
n**	7	3	16	16	18	31	22	14	4	12	14	18
IF	6	3	9	8	17	18	12	6	2	11	13	18
SF	7	5	9	6	9	11	7	3	3	9	5	8
$\overline{SF}$	2.17***	2.0	2.78	2.75	3.65	3.33	2.83	2.33	2.0	2.64	2.54	3.0
(±S.E.)	(±0.48)	(±0.58)	(±0.43)	(±0.45)	(±0.31)	(±0.28)	(±0.27)	(±0.42)	(±1.0)	(±0.2)	(±0.22)	(±0.27)
SI	6.13	4.50	5.95	4.4	6.14	4.62	3.70	2.97	2.67	4.70	3.41	5.72
H´	1.87	1.56	1.95	1.61	1.94	1.78	1.48	1.09	1.04	1.80	1.34	1.85
E	0.96	0.97	0.88	0.89	0.88	0.72	0.74	1.0	0.94	0.80	0.82	0.88

*Prevalence - percentage, out of stomach with some food.

**The abbreviations are denoted as follow: No. examined (n); No. with food (IF); No. food items (SF); Mean no. food items ($\overline{SF}$); Simpson's index (SI); Shannon-Weaver index (H´); Evenness (E).

***Mean (±S.E.).

Appendix X. Seasonal variations in food of cisco (age classes IV and V).

Months Food Items	J	F	M	A	M	J	J	A	S	O	N	D
Stickleback	0*	0	0	0	5.3	8.3	0	0	0	10.5	4.8	0
Copepoda	0	0	75	25	10.5	75	57.9	21.4	0	42.1	85.7	50
Mysis relicta	66.7	75	~25	75	10.5	16.7	15.8	7.1	100	47.4	9.5	6.3
Pontoporeia affinis	33.3	25	0	25	0	0	5.3	7.1	0	15.8	0	6.3
Hyallela azteca	0	0	0	0	42.1	0	5.3	7.1	~~0~~	0	0	0
Gammarus lacustris	0	0	0	0	36.8	8.3	5.3	57.1	0	15.8	9.5	6.3
Ephemeroptera (L)	0	0	0	0	47.4	8.3	10.5	7.1	0	0	4.8	0
Ephemeroptera (a)	0	0	0	0	0	0	5.3	7.1	0	0	0	6.3
Odonata	0	0	0	0	5.3	0	0	0	0	0	0	0
Diptera	0	0	0	0	0	0	0	7.1	0	0	0	0
Sphaeriidae	0	0	0	0	0	0	0	0	0	15.8	0	0
Fish Eggs	33.3	0	0	0	0	0	0	0	0	0	0	43.8
n**	29	17	25	18	21	30	32	25	26	26	31	43
IF	3	4	4	4	19	12	19	14	1	19	21	16
SF	3	2	2	3	7	5	7	8	1	6	5	5
$\overline{SF}$ (± S. E.)	1.33*** (±0.33)	1.0	1.0	1.25 (±0.25)	1.58 (±0.14)	1.17 (±0.11)	1.05 (±0.05)	1.29 (±0.13)	1.0	1.47 (±0.14)	1.14 (±0.1)	1.13 (±0.09)
SI	2.67	1.60	1.60	2.27	4.41	2.22	2.91	3.65	1.0	4.45	1.75	2.80
H'	1.04	0.56	0.56	0.95	1.64	1.13	1.44	1.06	0	1.63	0.90	1.21
E	0.94	0.79	0.79	0.85	0.82	0.66	0.69	0.76	1	0.90	0.49	0.72

Footnotes, see Appendix VII, for abbreviations and format.

Appendix XI. Intraintestinal distribution of *Metechinorhynchus salmonis* (and gravid females) in different age classes of lake whitefish

Age	Ave. Length of Intestine (mm)	No. Exam	Section of Intestine 1	2	3	4	5	6	7	8	9	10	Totals
2	123	31	0.27* (0)	0.6 (0)	0.4 (0)	0.4 (0)	0.23 (0)	0.13 (0)	0.57 (0.07)	0.93 (0.07)	1.6 (0.17)	0.73 (0.1)	5.86 (0.41)
3	167	24	4 (0.12)	6.16 (0.28)	4.32 (0.2)	3.88 (0.36)	1.08 (0)	0.6 (0.08)	0.84 (0.04)	4.68 (0.84)	6.56 (2.28)	1.84 (0.56)	33.96 (4.76)
4	196	46	6.67 (0.13)	13.0 (0.19)	6.83 (0.44)	5.71 (0.48)	2.08 (0.21)	1.52 (0.08)	1.79 (0.13)	9.35 (2.44)	10.35 (4.23)	1.63 (0.73)	58.93 (9.06)
5	220	59	21.46 (0.54)	34.41 (1.41)	19.47 (1.05)	10.92 (0.98)	3.92 (0.09)	2.53 (0.05)	3.10 (0.47)	9.93 (2.78)	10.69 (3.97)	2.73 (1.32)	119.16 (12.66)
6	248	36	20.2 (0.4)	30.68 (0.86)	15.78 (1.05)	9.84 (1.0)	3.41 (0.38)	2.35 (0.05)	2.92 (0.3)	10.73 (2.38)	11.0 (2.97)	1.38 (0.35)	108.29 (9.74)
7	269	40	25.8 (0.68)	53.4 (1.75)	21.9 (1.0)	13.75 (1.3)	4.3 (0.25)	2.28 (0.05)	2.6 (0.08)	11.5 (2.08)	9.68 (3.65)	2.45 (0.73)	147.66 (11.75)
8	277	76	35.3 (1.13)	58.11 (1.62)	26.05 (1.49)	15.92 (1.51)	5.61 (0.32)	3.42 (0.08)	3.13 (0.14)	10.23 (1.75)	8.2 (2.24)	2.42 (0.53)	168.44 (10.81)
9	283	66	41.3 (2.47)	99.3 (4.89)	41.86 (3.2)	22.39 (2.83)	7.73 (0.67)	4.91 (0.21)	2.83 (0.2)	8.21 (1.76)	7.64 (0.71)	2.14 (0.44)	238.31 (17.38)

*mean no. of *M. salmonis*
(mean no. of gravid females)

Appendix XII. Intraintestinal distribution of *Metechinorhynchus salmonis* (and gravid females) in group A lake whitefish taken at different seasons

Month	No. Exam	Section of Intestine 1	2	3	4	5	6	7	8	9	10	Totals
J	8	26.3* (0.1)	43.1 (1.0)	21.1 (0.4)	12.4 (0.5)	5.8 (0)	1.8 (0.1)	1.8 (0.1)	7.0 (2.8)	8.6 (4.9)	1.9 (0.9)	129.8 (10.8)
F	2	8.0 (0)	24.5 (0)	17.5 (0)	17.5 (0)	6.0 (0)	2.0 (0)	0.5 (0)	8.5 (0.5)	7.0 (2.5)	1.0 (0.5)	92.5 (3.5)
M	6	13.5 (0)	20.2 (0)	12.5 (0.5)	7.2 (0.2)	3.8 (0)	2.5 (0.2)	2.2 (0.2)	10.0 (2.2)	11.2 (3.2)	4.8 (2.0)	87.9 (8.5)
A	4	12.3 (0)	17.0 (1.0)	10.0 (1.5)	7.5 (0.5)	1.8 (0)	0.8 (0)	0 (0)	8.5 (1.8)	10.8 (6.0)	2.5 (1.0)	71.2 (11.8)
M	15	13.8 (0.1)	32.6 (1.2)	12.9 (1.7)	6.3 (1.5)	1.8 (0.3)	0.6 (0)	0.8 (0.1)	7.9 (3.5)	9.4 (3.9)	1.1 (0.4)	87.2 (12.7)
J	16	11.5 (0.3)	16.9 (0.6)	9.4 (0.6)	7.9 (0.3)	2.8 (0.8)	1.3 (0.1)	1.0 (0)	5.6 (1.1)	9.3 (3.6)	2.3 (0.9)	68 (8.3)
J	10	8.0 (0.3)	18.6 (1.6)	12.0 (0.7)	7.5 (0.1)	2.9 (0.1)	3.4 (0.1)	1.4 (0.4)	11.4 (3.4)	9.1 (2.2)	1.5 (0.4)	75.8 (9.3)
A	8	1.6 (0)	10.4 (0.6)	10.5 (1.3)	8.5 (1.6)	2.0 (0.1)	2.6 (0.1)	4.0 (0.4)	23.8 (6.3)	21.8 (5.4)	3.5 (0.6)	88.7 (16.4)
S	6	21.0 (1.0)	14.3 (0.7)	7.8 (0.8)	5.3 (0.3)	1.3 (0)	1.7 (0)	1.7 (0)	8.5 (1.7)	15.2 (7.2)	3.7 (1.8)	80.5 (13.5)
O	3	16.3 (0)	13.0 (0)	7.0 (0)	3.0 (0)	1.3 (0)	0 (0)	1.0 (0.3)	2.0 (0)	9.7 (6.7)	2.0 (1.7)	55.3 (8.7)
N	6	10.7 (0.2)	19.0 (0.2)	10.5 (0.5)	6.3 (0.3)	2.7 (0)	2.0 (0)	0.1 (0)	7.8 (1.8)	13.0 (4.5)	1.3 (0.3)	74 (7.8)
D	21	21.4 (0.1)	31.7 (1.1)	22.0 (0.9)	11.9 (1.0)	5.0 (0.05)	3.8 (0.05)	6.1 (0.7)	11.0 (3.[illegible])	8.1 (3.8)	1.9 (1.1)	122.9 (11.9)

*Mean no. of *M. salmonis*
(Mean no. gravid female)

Appendix XIII.* Intraintestinal distribution of *Metechinorhynchus salmonis* (and gravid females) in group B lake whitefish taken at different seasons

Month	No. Exam	Section of Intestine 1	2	3	4	5	6	7	8	9	10	Totals
J	7	30.4* (0.3)	77.0 (1.0)	26.4 (1.1)	15.0 (1.3)	6.0 (0.1)	4.3 (0)	2.9 (0.3)	12.3 (3.4)	10.0 (5.3)	3.3 (0.9)	187.6 (13.7)
F	3	24.0 (0)	59.0 (0.7)	36.3 (0.7)	22.7 (0.7)	8.0 (0.3)	4.0 (0)	4.7 (0)	13.3 (0.7)	8.3 (0.3)	1.3 (0.3)	181.6 (3.7)
M	16	33.4 (0.6)	45.4 (1.0)	22.9 (1.2)	19.1 (1.5)	4.0 (0)	2.4 (0)	1.5 (0)	12.2 (1.7)	7.8 (1.6)	2.8 (0.3)	151.5 (8.0)
A	7	18.7 (0.1)	34.0 (0.7)	11.0 (0.7)	4.3 (1.0)	2.1 (0)	1.3 (0)	1.1 (0)	5.7 (0.4)	3.4 (0.6)	1.3 (0.4)	82.9 (3.9)
M	8	33.6 (4.0)	51.3 (3.4)	18.1 (2.5)	12.0 (2.4)	6.9 (1.1)	1.8 (0.1)	1.5 (0.6)	4.0 (0.8)	2.0 (1.0)	0.4 (0.3)	131.6 (16.2)
J	7	24.0 (0.1)	60.1 (1.7)	19.7 (1.1)	12.9 (1.6)	6.9 (0)	7.1 (0)	7.6 (0)	15.4 (0.9)	6.9 (2.1)	4.1 (0.7)	164.7 (8.2)
J	8	41.3 (2.4)	114.5 (3.8)	55.3 (1.9)	29.5 (2.3)	42.6 (0.1)	7.4 (0)	7.8 (0)	23.5 (2.5)	22.3 (2.4)	4.1 (0.5)	348.3 (15.9)
A	11	20.0 (1.4)	19.3 (0.3)	13.4 (1.0)	9.0 (1.0)	4.4 (0.6)	1.5 (0.2)	1.4 (0.1)	10.5 (4.0)	13.5 (6.5)	3.9 (1.5)	96.9 (16.6)
S	4	39.0 (1.8)	32.3 (4.0)	13.0 (2.8)	8.3 (1.8)	2.5 (0)	1.0 (0.3)	3.3 (0.3)	3.0 (0.8)	2.5 (0.5)	0.5 (0.5)	105.4 (12.8)
O	12	20.8 (0.3)	44.7 (2.0)	17.0 (1.5)	8.2 (0.3)	2.8 (0)	1.9 (0)	0.8 (0)	8.3 (1.6)	10.0 (4.4)	1.8 (0.3)	116.3 (10.4)
N	14	20.1 (1.4)	59.7 (1.1)	21.1 (1.1)	14.7 (2.6)	3.5 (0.4)	1.2 (0.1)	2.9 (0.3)	10.4 (1.5)	10.1 (2.4)	2.0 (0.4)	145.7 (11.3)
D	18	56.8 (0.8)	91.7 (1.2)	32.2 (0.9)	21.3 (1.7)	6.8 (0.5)	4.2 (0.1)	3.9 (0.1)	10.6 (2.1)	5.6 (1.3)	2.3 (0.6)	235.4 (9.3)

*Mean no. of *M. salmonis*
(Mean no. gravid females)

Appendix XIV. Intraintestinal distribution of *Metechinorhynchus salmonis* (and gravid females) in cisco taken at different seasons

Month	No. Exam	Section of Intestine										Totals
		1	2	3	4	5	6	7	8	9	10	
J	27	0.9* (0.1)	2.0 (0.1)	2.1 (0.4)	1.3 (0.1)	0.7 (0)	0.8 (0)	1.3 (0.4)	2.5 (1.0)	3.0 (1.5)	0.6 (0.4)	15.2 (4.0)
F	20	1.3 (0.6)	1.6 (0.3)	2.1 (0.8)	1.3 (0.7)	0.6 (0.1)	0.7 (0.1)	1.3 (0.5)	2.6 (1.5)	1.9 (1.0)	0.9 (0.2)	14.3 (5.8)
M	14	0.4 (0)	0.8 (0)	0.7 (0.4)	1.2 (0.3)	0.1 (0)	0.4 (0)	0.4 (0.1)	0.6 (0.3)	1.7 (0.8)	0.1 (0.1)	6.4 (2.0)
A	6	1.7 (0)	3.8 (0.8)	4.2 (1.5)	2.8 (0.8)	1.5 (0.5)	0.2 (0)	1.3 (0.2)	2.2 (0.8)	2.7 (0.7)	0.7 (0.2)	21.1 (5.5)
M	7	0.1 (0)	0.3 (0)	0.4 (0)	0.7 (0)	0.1 (0)	0.6 (0)	0.1 (0)	0.1 (0)	2.3 (1.3)	2.4 (0.4)	7.1 (1.7)
J	36	0.3 (0.03)	0.6 (0.5)	1.1 (0.4)	0.8 (0.1)	0.03 (0)	0.1 (0)	0.5 (0.1)	1.1 (0.7)	1.7 (0.8)	0.3 (0.5)	6.5 (3.1)
J	57	0.9 (0.2)	1.5 (0.4)	1.4 (0.2)	0.5 (0.2)	0.2 (0.04)	0.3 (0.1)	0.5 (0.1)	1.3 (0.6)	1.8 (0.7)	0.4 (0.1)	8.8 (2.6)
A	57	0.5 (0.04)	1.0 (0.2)	0.9 (0.2)	1.1 (0.5)	0.5 (0.04)	0.2 (0.04)	0.4 (0.2)	2.0 (1.0)	3.1 (1.5)	0.7 (0.2)	10.4 (3.9)
S	38	0.4 (0)	0.8 (0.1)	0.8 (0.4)	0.6 (0.2)	0.2 (0.1)	0.3 (0.03)	0.2 (0.2)	1.0 (0.4)	1.8 (0.9)	1.0 (0.4)	7.1 (2.7)
O	34	2.9 (0.8)	3.8 (1.0)	2.6 (0.7)	1.8 (0.5)	0.9 (0.2)	0.5 (0.03)	0.7 (0.2)	1.4 (0.9)	3.2 (1.9)	0.8 (0.3)	18.6 (6.5)
N	49	1.4 (0.4)	2.4 (1.0)	2.4 (0.7)	1.7 (0.6)	0.6 (0.1)	0.7 (0.1)	1.1 (0.4)	2.1 (0.8)	2.0 (1.0)	1.0 (0.4)	15.4 (5.5)
D	53	0.8 (0.1)	1.0 (0.1)	1.21 (0.2)	0.9 (0.3)	0.6 (0.2)	0.6 (0.02)	0.9 (0.1)	1.6 (0.6)	3.2 (1.6)	1.0 (0.4)	11.8 (3.6)

*Mean no. of *M. Salmonis*
(Mean no. gravid females)